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COVER: The stylized representation of fruits of various Leguminosae, forming the design of our new cover for Volume 59, is based on material from plants growing in the Arnold Arboretum of Harvard University. The design was planned and executed by Karen S. Velmure, who has also drawn several of the preceding covers as well as various devices used in the *Journal of the Arnold Arboretum* and on the offprint covers.

The three subfamilies of the Leguminosae are represented by the fruits shown in the design. The genera are, top row (left to right), *Albizia* (Mimosoideae), *Gleditsia* (Caesalpinioideae), *Caragana* (Faboideae), *Gymnocladus* (Caesalpinioideae), and lower row, right, *Colutea* (Faboideae).

The family Leguminosae, the second most important family of flowering plants, is to be the subject of an International Legume Conference at the Royal Botanic Gardens, Kew, Richmond, Surrey, England, in July, 1978. This cover is our salute to the complete success of that Conference.

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FOSSIL DICOTYLEDONOUS WOODS FROM YELLOWSTONE NATIONAL PARK, II

ELISABETH F. WHEELER, RICHARD A. SCOTT, AND ELSO S. BARGHOORN

THIS PAPER is the second in a series dealing with silicified dicotyledonous woods from two regions of Yellowstone National Park, Wyoming and Montana. In the earlier paper (Wheeler, Scott, & Barghoorn, 1977), we described eight species of fossil woods in five genera (*Alnus*, *Carpinus*, *Ulminium*, *Magnoliaceoxylon*, and *Plataninium*). Species in nine additional genera are described here; other dicotyledonous woods will be described in a third paper which will include floristic and paleoecological discussions.

In Yellowstone National Park, silicified woods occur most prominently in the striking succession of fossil forests at Specimen Ridge and Amethyst Mountain along the Lamar River, and in the Gallatin area some 40 miles to the northwest in Montana. The fossil forests in both areas are in volcaniclastic rocks of the Absaroka volcanic field. The Amethyst Mountain and Specimen Ridge fossil forests are in the Lamar River Formation; the Gallatin forests are in the Sepulcher Formation. These two formations intergrade laterally and are of late early to early middle Eocene age (Smedes & Prostka, 1972). Detailed locality information was given in our first paper (Wheeler, Scott, & Barghoorn, 1977) on these fossil woods.

ANACARDIACEAE

Rhus crystallifera Wheeler, Scott, & Barghoorn, sp. nov. FIGURES 1–3.

Growth rings. Present, distinct, 1–3.5 mm. wide.

Vessel elements. Semi-ring porous, transition from earlywood to latewood gradual; extent of earlywood zone variable; pores mostly solitary and round in outline, some multiples of 2 to 3 and clusters present; tangential diameter of earlywood pores 105–205 μm., mean 175 μm.; radial diameter of earlywood pores 118–210 μm., mean 178 μm.; tangential diameter of latewood pores 40–100 μm., mean 60 μm.; radial diameter of latewood pores 38–125 μm., mean 80 μm.; length 275–460 μm.; perforation plates simple; intervascular pitting crowded alternate, to 10 μm. across; pits to parenchyma horizontally elongate and irregular in shape; tyloses present.

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Parenchyma. Paratracheal, vasicentric, generally with 4 cells per strand.

Rays. Mostly 1 to 2 cells wide, rarely 3 cells wide; heterocellular; almost all rays with inflated crystalliferous cells, in radial section these appearing twice the size of non-crystalliferous cells; multiseriate rays 6 to 27 cells, 92–600 μm. high.

Imperforate tracheary elements. Septate fibers present.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054A-14, measuring 70 × 95 × 150 mm.

LOCALITY. Amethyst Mountain, U.S.G.S. Paleobot. Loc. No. D-2054A.

Both the Anacardiaceae and Burseraceae have species with the combination of characters descriptive of this fossil; that is, pores solitary, rounded, and in radial multiples, simple perforations, vessel–ray pitting simple and variable in outline, paratracheal parenchyma, septate fibers, and narrow crystal-containing rays. The similarity of the wood anatomy of these two families is well known and is used as evidence of their close relationship (Heimsch, 1942; Webber, 1941).

The Yellowstone wood is semi-ring porous. No members of the Burseraceae are known to show any tendency to ring porosity, while ring porosity is known in the tribes Spondieae and Rhoideae of the Anacardiaceae (Heimsch, 1942). Unilaterally compound vessel–ray pitting, a feature not observed in the fossil, is a distinguishing characteristic of the Burseraceae (Brett, 1966). For these reasons, we consider the fossil to be a member of the Anacardiaceae.

Spondias axillaris Roxb. is the only member of the Spondieae in which ring porosity has been observed. We examined sections of this species and *S. mombin* L. Both have very wide rays (up to 6 to 8 cells wide), some rays have intercellular canals, and there are no more than two vessels per pore multiple. *Pistacia*, *Cotinus*, and *Schmaltzia* are ring porous members of the Rhoideae, but pore distribution and ray structure of these genera appear different than in the fossil. The anatomy of the fossil and extant species of *Rhus* is similar: the subgenus TOXICODENDRON is the only subgenus of *Rhus* reported to contain septate fibers, and septate fibers are present in the fossil (Heimsch, 1940); crystals are more common in the fossil wood than in any extant *Rhus* examined, but in all other features the fossil's anatomy is consistent with that of extant species of *Rhus*.

The numerous reports of fossil woods of the Anacardiaceae, most from Old World localities, are listed in papers by Awasthi (1965) and Kramer (1974). Fossil woods presumed to have affinities with *Rhus* have been assigned to *Rhoidium* Unger (1850). Three species, *Rhoidium juglandifolia* Unger, *R. ungeri* Mercklin, and *R. philippense* Orie, are known. All were described in the middle of the 19th century, a time when descriptions of fossil woods were very brief and generally unaccompanied by illustrations. Consequently, detailed comparison of the Yellowstone fossil wood with

these species is not possible. Without examination of the type material, it is also impossible to determine whether the woods called *Rhoidium* have any relationship to *Rhus* or the Anacardiaceae.

Among the oldest known woods of the Anacardiaceae are those reported from the Eocene Eden Valley, Wyoming, locality (Kruse, 1954). The two species described from this locality are quite different from the Yellowstone wood. *Schinoxylon actinoporosum* Kruse is diffuse porous and has radial chains of up to 25 pores, no axial parenchyma, and intercellular canals in the rays. This wood was said to resemble *Schinus* in those features seen in longitudinal sections; however, it does not have the distinctive ulmiform pore distribution of extant species of *Schinus*. It is unclear why this wood was assigned a name implying affinities with *Schinus*, as the Eden Valley specimen lacks the pore distinction diagnostic of this genus. The second species from Eden Valley, *Edenoxylon parviareolatum* Kruse, does not resemble any one extant genus of the Anacardiaceae. It is diffuse porous and has numerous small vessels; the rays commonly have intercellular canals. This species was subsequently reported from the lower Eocene of Herne Bay, Kent, England (Brett, 1966). These two species, a wood assigned to *Tapirira* from the Clarno beds of Oregon (Manchester, 1976), and *Anacardioxylon magniporosum* Platen (1908) from California are the only fossil woods of the Anacardiaceae known from the United States.

No Anacardiaceae are reported from the Kisinger Lakes–Tipperary flora (MacGinitie, 1974). A member of the tribe Spondieae is reported from the Golden Valley Formation, latest Paleocene age (list prepared by Hickey in Leopold & MacGinitie, 1972). *Rhus* is on a preliminary list of megafossils from the Wind River Formation, late early Eocene age (MacGinitie, 1969), and it is also reported from the Wagon Bed Formation of middle Eocene age (Leopold & MacGinitie, 1972). Two species of *Rhus* and one of *Toxicodendron* occur in the Green River flora (MacGinitie, 1969). There are two species of *Rhus* in the Florissant flora (MacGinitie, 1953).

There are 15 species in the subgenus TOXICODENDRON (Brizicky, 1962). They are mostly temperate North American and Asian in distribution, although *Rhus striata* Ruiz & Pavon grows in tropical South America.

CYRILLACEAE

Cyrilloxylon eocenicum Wheeler, Scott, & Barghoorn, sp. nov.
FIGURES 4–7.

Growth rings. Present, distinct, 2–5 mm. wide.

Vessel elements. Predominantly solitary, some pairs, angular in outline; gradually decreasing in size through the growth ring, with a tendency to form a band of pores at the beginning of the growth increment; tangential diameter of earlywood vessels 56–85 μm., mean 70 μm.; radial diameter 67–102 μm., mean 85 μm.; tangential diameter of latewood vessels 33–66

μm., mean 47 μm.; 53 to 78 per square mm.; length 670–875 μm.; perforation plates scalariform, generally with more than 40 bars; intervascular pitting usually opposite but sometimes transitional and scalariform; vessel–ray pits similar to intervascular pitting.

Parenchyma. Not observed.

Rays. 1 to 7 cells wide, multiseriates with a single marginal row of square and upright cells, a few homocellular rays; multiseriates 9 to 32 cells, 164–800 μm. high; uniseriates rare, composed of upright cells, 2 to 19 cells high.

Imperforate tracheary elements. Fiber tracheids with small bordered pits.

MATERIAL. Two specimens of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-28, measuring 52 × 68 × 45 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

There are many plants which have wood with small angular vessels, scalariform perforation plates, and opposite and scalariform pitting. However, the occurrence of these structural features in combination with multiseriate rays more than three cells wide that often have a single marginal row of upright cells and rare uniseriate rays is not common. Such structural features are characteristic of the Cyrillaceae. The wood described here also resembles *Cornus*, a genus that has been reported from the Yellowstone compression flora (Dorf, 1960) and from other Tertiary floras of the Rocky Mountains (Leopold & MacGinitie, 1972). *Cornus* differs from the wood described here and from *Cyrilla* as it has numerous uniseriate rays and markedly heterocellular rays.

Slides of six specimens of *Cyrilla racemiflora* were examined. As might be expected for such a wide-ranging species (southeastern United States to the Amazon), there is considerable structural variability. Maximum ray width ranges from four to eight cells, and parenchyma abundance and distinctiveness of the growth rings varies. One specimen (Hw 19068) from the Amazon has ill-defined growth increments, while some specimens from the southeastern United States tend toward being semi-ring porous. Thomas (1960) earlier noted the absence of distinct growth rings in *Cyrilla* wood from the more tropical parts of the range of the genus. The fossils resemble those woods from the northern part of *Cyrilla*'s range as they tend toward semi-ring porosity and have distinct growth rings.

There are two other genera in the Cyrillaceae, *Purdiaea* and *Cliftonia*. *Purdiaea* (two specimens examined) differs from the Yellowstone wood as it has relatively numerous uniseriate rays. Van der Burgh (1964) and we observed that rays in *Cliftonia* have more marginal rows of square and upright cells than do rays in *Cyrilla*. The rays of the Yellowstone wood resemble *Cyrilla* more than *Cliftonia* as they generally have but a single marginal row of square and upright cells. *Cliftonia* has less parenchyma

than *Cyrilla*. The amount and distribution of parenchyma in the fossil was difficult to assess because of the relatively poor preservation. It is possible that the Yellowstone wood may resemble *Cliftonia* more than *Cyrilla* by having scanty parenchyma. Consequently, as the fossils may be intermediate in structure between these two genera, we assign them to *Cyrilloxylon*. The two specimens assigned to this taxon, D-2054B-28 and -35, differ slightly. D-2054B-35 has wider growth rings, vessel diameter does not change as much throughout the growth ring, and its vessel elements are slightly longer (up to 920 μm.), than D-2054B-28.

Fossil wood of the Cyrillaceae has been reported from the Brandon Lignite of Vermont (Spackman, 1949) and the brown coals of the Netherlands (van der Burgh 1964, 1973). The Brandon *Cyrilla* has 20 to 25 bars per perforation plate, vessel elements 550–650 μm. long, and rays up to 5 cells wide with pronounced margins of upright cells. *Cyrilloxylon europaeum* van der Burgh lacks growth rings, its perforation plates have 15 to 30 bars, and its rays are up to 5 cells wide with 1 to 7 marginal rows of upright cells. This species appears intermediate between *Cyrilla* and *Cliftonia* as the abundant parenchyma is *Cyrilla*-like, but the rays are *Cliftonia*-like.

The Cyrillaceae, a New World family of subtropical and warm-temperate areas, has three genera: *Cyrilla*, *Cliftonia*, and *Purdiaea*. *Cyrilla*, a monotypic genus, grows in acid soils along the margins of swamps and streams and in wet pinelands. In this country, it occurs in the coastal pine belt from Florida to southeast Virginia to southeast Texas; it is also present in Mexico, British Honduras, the West Indies, and northern South America. *Cliftonia* has a more restricted distribution and occurs in the Coastal Plain of Georgia, Florida, Alabama, and Mississippi. *Purdiaea* is found in Venezuela, Colombia, Peru, Cuba, and the Isle of Pines (Thomas, 1960, 1961).

There is no previous record of Cyrillaceae in the Rocky Mountains, as far as we know.

FAGACEAE

Quercinium amethystianum Wheeler, Scott, & Barghoorn, sp. nov.
FIGURES 8, 9.

Growth rings. Present, 2.5–4.5 mm. wide, not always distinct.

Vessel elements. Semi-ring porous; solitary, circular to oval in outline; in broad radial bands; tangential diameter of earlywood pores 110–200 μm., mean 140 μm.; radial diameter 165–265 μm., mean 225 μm.; tangential diameter of latewood 33–94 μm., mean 64 μm.; length to 494 μm.; perforation plates simple; intervascular pitting alternate; vessel–ray pits variable, typically large, and often vertically elongate; tyloses present.

Parenchyma. Abundant, in 1- to 4-cell-wide bands, appearing wavy in cross section, particularly in the latewood; as isolated cells; and in the earlywood intermingled with tracheids forming conjunctive tissue between the vessels and rays, not swollen crystalliferous.

Rays. Rays of two distinct sizes, uniseriate (rarely biseriate), aggregate and compound; homocellular and heterocellular with marginal rows of square and upright cells, uniseriates 2 to 20 cells, 47–360 μm. high; large rays to 31 cells broad and up to 8 mm. high.

Imperforate tracheary elements. Vasicentric tracheids with pitting on radial and tangential walls, and fiber tracheids with bordered pits.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054A-11, measuring 41 × 50 × 120 mm.

LOCALITY. Amethyst Mountain, U.S.G.S. Paleobot. Loc. No. D-2054A.

Wood of certain evergreen oaks may be distinguished from deciduous oaks, as the wood of the former group is diffuse or semi-ring porous and has aggregate, rather than composite, rays in the mature wood (Williams, 1942; Brett, 1960). The wood of *Lithocarpus* is indistinguishable from the wood of such evergreen oaks. Brett (1960) emended the organ genus *Quercinium* Unger so that it would encompass species of fossil wood with evergreen oak-*Lithocarpus* structure. The specimen described here, because it is semi-ring porous, is assigned to *Quercinium*. The name *Quercoxylon* Kräusel (1939) emend. Müller-Stoll & Mädel (1957) is also used for fossil oak woods; however, *Quercinium* has priority.

Three species of fossil oak wood have been described from the Yellowstone fossil forests: *Quercus rubida* Beyer (1954), *Quercinium knowltonii* Felix (1896), and *Q. lamarense* Knowlton (1899). *Quercus rubida* Beyer is distinct as it is ring porous with an abrupt transition from a well-defined earlywood zone to the latewood zone, while the two species of *Quercinium* have evergreen oak-*Lithocarpus* structure.

The description of the earliest-named species, *Quercinium knowltonii* Felix, is quite brief. It was described as having oval earlywood vessels with a tangential diameter of up to 210 μm., latewood vessels with a tangential diameter of 80–120 μm., and parenchyma in short uniseriate bands associated with the pores. The only illustration accompanying the diagnosis of *Q. knowltonii* is a schematic drawing of a transverse section. A detailed comparison of *Q. amethystianum* with *Q. knowltonii* is not possible, but the parenchyma distribution in the two seems distinct and warrants the use of a different name for the specimen described above. An emended diagnosis of *Q. lamarense* follows, and differences between it and *Q. amethystianum* will be discussed following that diagnosis.

Quercinium lamarense Knowlton, emend. Wheeler, Scott, & Barghoorn
FIGURES 10–12.

Growth rings. Present, 2–10 mm. wide, not always distinct.

Vessel elements. Semi-ring porous; solitary, oval in outline in earlywood, circular in outline in latewood; arranged in flamelike, radial pattern; tan-

gential diameter of earlywood pores 80–250 μm., mean 200 μm.; radial diameter of earlywood pores 195–320 μm., mean 240 μm.; tangential diameter of latewood pores 50–120 μm., mean 90 μm.; length to 645 μm.; perforation plates simple; intervascular pitting alternate, pit-pairs circular in outline; vessel–ray pits large, and often vertically elongate; tyloses present, but infrequent.

Parenchyma. Predominantly apotracheal, in distinct bands 1 cell wide, at times 3 cells wide (within some growth rings these parenchyma bands more closely spaced in the earlywood), as isolated cells, and as broken uniseriate lines; also paratracheal; not swollen crystalliferous.

Rays. Rays of two distinct sizes, uniseriate (occasionally partially biseriate) and aggregate; homocellular and less frequently heterocellular with marginal rows containing some square and upright cells; uniseriates 2 to 20 cells, 64–460 μm. high, numerous, 13–17 per mm.; aggregate rays to 1 mm. broad and 8 mm. high; units of aggregate rays, mostly 8-cell-wide rays.

Imperforate tracheary elements. Vasicentric tracheids with pitting on radial and tangential walls, and fiber tracheids with bordered pits smaller and less frequent than on the vascular tracheids.

MATERIAL. 12 specimens of mature, silicified secondary xylem.

HOLOTYPE. 2 slides: USNM 245721 a and USNM 245721 b.

LOCALITY. Specimen Ridge.

One of the most common dicotyledonous woods in the collections from Specimen Ridge is this species of *Quercinium*. We have examined sections of seven specimens collected by Scott and an additional five specimens collected by Knowlton and Read that belong to the National Museum and the U.S. Geological Survey. The original diagnosis of *Q. lamarense* Knowlton (1899) is quite brief and is accompanied by four line drawings. All the drawings are at a fairly high magnification showing in detail a few pores, but not showing overall pore or parenchyma distribution. Quantitative data were given only for the vessels.

In his monograph on the Yellowstone fossil forests, Knowlton wrote that the material he described as *Quercinium lamarense* came from an upright stump measuring four feet in diameter and was collected on August 22, 1887. Among Knowlton's collections housed at the National Museum, there are two slides (numbers 149 and 150) described in his notebooks as sections from an upright stump measuring four feet in diameter collected on that date. As collection data are identical and these two slides are the only ones of oaks in Knowlton's slide collection, it seems safe to assume these are the sections which Knowlton described and figured, and so we designate them the type of *Quercinium lamarense* Knowlton, emend. Wheeler, Scott, & Barghoorn.

Knowlton acknowledged that *Quercinium lamarense* is similar to the

earlier-described *Q. knowltonii* Felix (1896), but he suggested that the shape and size of the pores were different. It is possible that *Q. knowltonii* and *Q. lamarense* are different names applied to the same type of wood. However, as the original material Felix described was not available for study, we are using the name *Q. lamarense* for the woods we have examined.

Quercinium amethystianum has more parenchyma than *Q. lamarense*, and aggregate and compound rays rather than just aggregate rays as does *Q. lamarense*.

Ring porous oak woods are among the most commonly described fossil woods, perhaps due in part to the ease of recognizing their distinctive wood structure. Reports of fossil woods resembling evergreen oaks and *Lithocarpus* are not as numerous. Lists of the occurrence of fossil oak woods have been prepared by Prakash and Barghoorn (1961a), Müller-Stoll and Mädel (1957), and Privé (1975). There are five species of fossil wood of the evergreen oak type known from the United States, all from the Tertiary of California. Four species, *Quercinium anomalum*, *Q. solerederi*, *Q. wardii*, and *Q. lesquereuxii*, were described by Platen (1908). The fifth species, *Quercus ricardensis* Webber (1933), is from the Ricardo Pliocene. All five differ from *Quercinium amethystianum* and *Q. lamarense* in pore size and/or parenchyma abundance.

Williams (1942) found in North American oaks a loose correlation between crystal abundance in wood and dryness of habitat: generally the dryer the habitat, the more common the crystals. Neither *Quercinium amethystianum* nor *Q. lamarense* has crystalliferous parenchyma.

Oak leaves are abundant in the Yellowstone compression flora (Dorf, 1960, 1964). No species of *Quercus* are reported from the Kisinger Lakes-Tipperary flora (MacGinitie, 1974), but there are oaks in the older Lost Cabinian Wind River flora and the younger Green River flora.

JUGLANDACEAE

Pterocaryoxylon knowltonii Wheeler, Scott, & Barghoorn, sp. nov.
FIGURES 13–15.

Growth rings. Distinct, 5–6.5 mm. wide, visible to unaided eye, demarcated by 3 to 6 rows of flattened, thick-walled, imperforate tracheary elements.

Vessel elements. Semi-ring porous; mostly solitary or in radial multiples of 2 to 4; earlywood pores and pore multiples in diagonal arrangement; solitary pores oval in outline; latewood pores tending to be squared off, but not highly angular; tangential diameter of earlywood pores 160–310 μm., mean 215 μm.; radial diameter of earlywood pores 225–400 μm., mean 325 μm.; tangential diameter of latewood pores 70–140 μm., mean 118 μm.; radial diameter 110–190 μm., mean 165 μm.; length 460–850 μm.; perforation plates simple; intervascular pitting alternate, pits 10–12 μm. across; vessel–ray pits not observed; tyloses present.

Parenchyma. Apotracheal, as short uniseriate lines in cross section, scanty in earlywood, more frequent in latewood with lines of greater tangential extent more closely spaced.

Rays. Multiseriates to 3 cells wide, 5 to 26 cells, 155–515 μm. high; with uniseriate margins of 1 to 8 (mostly 1 to 3) rows of square and upright cells; uniseriates 3 to 14 cells, 105–385 μm. high, cells of uniseriate rays similar in shape to uniseriate margins of multiseriate rays; 6 to 9 per mm.

Imperforate tracheary elements. Pitting not observed.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-37, measuring 35 × 24 × 41 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

The fossil resembles the wood of *Pterocarya* and *Juglans* sections CARDIOCARYON (oriental butternuts) and TRACHYCARYON (*J. cinerea*, the American butternut). Wood of the black walnuts, both tropical and temperate, is distinguished by ray cell shape, the presence of crystalliferous parenchyma strands, and the reticulate thickenings in the vessel elements (Miller, 1976a, 1976b).

The rays in the fossil are three cells wide. Rays only two cells wide were observed in the five specimens of *Pterocarya rhoifolia*; three-cell-wide rays occur in *Juglans*. Kribs (1927) noted rays are only one to two cells wide in *Pterocarya*. We examined four species of *Pterocarya* in the Harvard Wood Collection and observed some occasional three-cell-wide rays in one preparation of *P. paliurus*. Müller-Stoll and Mädel (1960) reported these rays in *Pterocarya caucasia* C. A. Meyer. The three-cell-wide rays of the Yellowstone fossil are more suggestive of *Juglans* than *Pterocarya*, as such rays are rare in the former. However, there are ten species of *Pterocarya* (Willis, 1973), and examination of all species is necessary to determine if ray width is a useful feature for separating *Juglans* and *Pterocarya*.

One of the distinctive features of the fossil is the pronounced diagonal arrangement of the earlywood pores. Drs. Regis Miller and B. F. Kukachka of U.S.D.A. Forest Products examined thin-sections of the fossil and compared then to sections of *Juglans* and five specimens of *Pterocarya rhoifolia*. Drs. Miller and Kukachka did not observe diagonal pore arrangement in any extant species of *Juglans*, but did in the five specimens of *P. rhoifolia*. Diagonal pore arrangement also occurs in *P. paliurus*. Specimens of the other eight species of *Pterocarya* were not available for study. Drs. Miller and Kukachka suggest that the fossil resembles *Pterocarya* more than *Juglans*, a suggestion with which we concur.

Müller-Stoll and Mädel (1960) established the genus *Pterocaryoxylon* for juglandaceous woods with the following characteristics: diffuse or semi-ring porous; vessels thin-walled, solitary, and in radial multiples of 2 to 4;

simple perforation plates; alternate intervascular pitting; parenchyma in one-cell-wide, short, irregularly spaced bands, and 1 to 3 seriate rays. As the Yellowstone wood exhibits these characteristics common to both *Juglans* and *Pterocarya*, we are naming it as a new species of this genus.

No fossil wood resembling *Pterocarya* has been previously described from the Tertiary of North America, although *Pterocarya* is among the genera of woods listed as occurring in the Miocene Vantage, Washington, fossil forests (Beck, 1945; Prakash, 1968). Only one species of fossil wood of *Juglans* has been described from North America. *Juglans fryxellii* Prakash & Barghoorn (1961b) from the Miocene Vantage forests resembles the extant black walnuts and is distinct from *Pterocaryoxylon* as it has crystalliferous parenchyma, smaller vessels, and no diagonal pore arrangement.

To date, five species of *Pterocaryoxylon* have been described. These are *P. pannonicum* from the Pliocene of Hungary, *P. honshouense* (originally called *Pterocarya rhoifolia* by Watari in 1952), *P. chinense* from the Tertiary of China, *P. pilinyense* from the Tertiary (Helvetian) of Hungary, and *P. subpannonicum* from the Pliocene of France (Privé, 1974). *Pterocaryoxylon honshouense* and *P. chinense* both have rays only 1 to 2 cells wide. *Pterocaryoxylon honshouense* also is characterized by pores in diagonals and so appears structurally similar to *Pterocarya*. *Pterocaryoxylon pilinyense* Greguss also has 1- to 2-cell-wide rays, but it has crystalliferous parenchyma, a feature not associated with *Pterocarya* or the butternuts. *Pterocaryoxylon pannonicum* and *P. subpannonicum* have rays to 3 cells wide, but do not show any evidence of diagonal pore arrangement. Woods assigned other generic names, but which might be transferred to *Pterocaryoxylon* include *Juglandinium caucasicum* Gaivoronsky from the Oligocene of the U.S.S.R., *J. tasseewii* Naschokin from the Tertiary of the U.S.S.R., and *Juglandoxylon* sp. Petrescu & Nuta from the Miocene of Rumania (Privé, 1974).

Both *Juglans* and *Pterocarya* are members of the Kisinger Lakes flora (MacGinitie, 1974), and both occur at many Tertiary localities in the Rocky Mountains. The history of *Pterocarya* in the Rocky Mountain region was summarized by Leopold and MacGinitie (1972).

MYRICACEAE

Myrica absarokensis Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 16–19.

Growth rings. Present, distinct.

Vessel elements. Diffuse porous; predominantly solitary, some pairs; tangential diameter 30–85 μm. (mean 50 μm.); radial diameter 47–118 μm., mean 75 μm.; 65–110 per square mm.; length 505–735 μm.; perforation plates all scalariform with 7 to 16 bars; intervascular pitting predominantly opposite, some transitional, vessel–ray pits similar to intervascular pitting.

Parenchyma. Apotracheal diffuse, as isolated strands, often inflated and crystalliferous.

Rays. Multiseriates to 4 cells wide; 4 to 25 cells, 80–600 μm. high; with uniseriate margins of 1 to 9 rows of square and upright cells; uniseriates 2 to 8 cells, 92–350 μm. high, apparently composed of only square and upright cells; 8 to 12 per mm.

Imperforate tracheary elements. Fibers with bordered pits on both radial and tangential walls.

MATERIAL. Five specimens of mature secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-11, measuring 75 × 59 × 50 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

There are five specimens assigned to this taxon (D2054B-11, -21, -23, -25, and -34). There is some variation in quantitative characters, particularly vessel density, but this sort of variation is not considered taxonomically significant. The minimum tangential diameter of a vessel element is 32 μm. in all specimens, the maximum tangential diameter varies from 60 to 87 μm., the mean varies from 46 to 57 μm.; vessel density ranges from 50 to 200 per square mm.; and the number of bars per perforation plate ranges from 6 to 20, although in all specimens it is most frequently 12. Vessel elements up to 1200 μm. long occur in some specimens.

The combination of characters of these woods (small solitary vessels, scalariform perforation plates, opposite intervascular pitting, and apotracheal diffuse parenchyma) occurs in many unrelated families, of which only four have an average vessel element length of less than 800 μm. These are the Hamamelidaceae, Cornaceae, Cyrillaceae, and Myricaceae.

In the Hamamelidaceae, vessel–ray pitting is typically large and elongate, and intervascular pitting is predominantly scalariform. The wood of the Cyrillaceae is characterized by perforation plates of 30 to 50 bars and few uniseriate rays; that of the Cornaceae, by perforation plates with many (more than 20) bars, multiseriate rays frequently higher than 1 mm., and no crystalliferous parenchyma. Metcalfe and Chalk (1950) report that *Kaliphora* and *Torricellia* have simple perforations, but Willis (1973) places *Torricellia* in its own family and notes that *Kaliphora*, which is indigenous to Madagascar, should probably be excluded from the Cornaceae. As the Yellowstone woods have small vessel–ray pitting, opposite intervascular pitting, less than 20 bars per perforation plate, low rays, and inflated crystalliferous parenchyma strands, they differ from members of these families. The structural features of these woods match those of the Myricaceae, and they are assigned to that family.

Slides of the wood of eight species of *Myrica* were examined. Of these species, the Yellowstone woods most closely resemble *M. cerifera* and *M. rubra*, as both have inflated crystalliferous axial parenchyma and predominantly scalariform perforation plates. Some species of *Myrica* do have

mostly or exclusively simple perforation plates and lack crystalliferous parenchyma.

Myricoxylon hungaricum Müller-Stoll & Mädel (1962) from the Miocene of Hungary differs from the Yellowstone wood as this Hungarian fossil wood lacks growth rings and has predominantly simple perforation plates and a higher ray density. Müller-Stoll and Mädel also noted the structural similarity of *Myrica* wood to wood of the Cornaceae and Hamamelidaceae and used number of bars per perforation plate and nature of vessel to ray parenchyma pitting to distinguish between these families.

Kruse (1954) described an Eocene fossil wood and referred it to the genus *Myrica*. This wood from Eden Valley, Wyoming, was described as having perforations with up to 35 to 40 bars, a larger number of bars than is characteristic of the extant Myricaceae. We prepared new sections of the type of *Myrica scalariformis* Kruse and observed the number of bars per perforation plate to range from 15 to 32, most commonly numbering 20 to 22 bars. This is more consistent with the anatomy of extant *Myrica* species. *Myrica scalariformis* differs from the Yellowstone wood as there are more bars per perforation plate, no crystalliferous axial parenchyma, a lower vessel density, and enlarged cells in the rays and the axial parenchyma. We did not observe enlarged parenchyma cells in any of the extant species of *Myrica* we examined, and such cells are not mentioned in descriptions of the anatomy of the family (Metcalfe & Chalk, 1950; Record & Hess, 1943). It is possible that the Eden Valley wood has been incorrectly assigned to *Myrica*.

There are numerous reports of putative *Myrica* leaves from Cretaceous and early Tertiary localities in North America. Chourey (1974) examined these reports in detail and found that most of these fossils cannot be considered to be *Myrica*. Identification of a leaf as *Myrica* requires use of venation pattern, leaf morphology, and cuticular features. As most of the putative *Myrica* species are represented by specimens that are either fragmentary, poorly preserved, or without cuticle, it is not possible to determine their affinities. Chourey suggests that, to date, there have been only eight occurrences of megafossils which are probably Myricaceae. Berry described many *Myrica* leaves from the Eocene of southeastern United States. His collections and new collections from this area were examined with especial care, but no *Myrica* leaves were found in either the original collections or the new ones.

Pollen of the Myricaceae is reported from a few North American Tertiary localities. According to Chourey, ". . . not until Eocene times is the family Myricaceae well established . . . The limited record of *Myrica* pollen, however, might also show a more authentic record of the evolution and distribution of *Myrica* throughout the Cretaceous and Tertiary than is indicated by common overuse of the generic name for fossil leaves." Wolfe (1973) noted that the history of the family is uncertain as its pollen is similar to other amentiferous families.

The Yellowstone wood represents one of the oldest occurrences of the family and the genus. It has primitive wood structure for the genus as it

has exclusively scalariform perforation plates.

Today *Myrica* has a nearly cosmopolitan distribution, but does not occur naturally in northern Africa, central and southeastern Europe, Australia, and southwest Asia (Willis, 1973). *Myrica cerifera*, a species which occupies a wide variety of habitats, has a remarkably wide range and grows in the southeastern United States, the larger islands of the West Indies, and parts of Mexico and Central America. *Myrica rubra* is a member of the mixed mesophytic and evergreen sclerophyllous broad-leaved forest associations of China (Wang, 1961).

Nyssaceae

Nyssa saximontana Wheeler, Scott, & Barghoorn, sp. nov.

Figures 20–23.

Growth rings. Present, distinct, 2–5.5 mm. wide.

Vessel elements. Diffuse porous; solitary and in radial multiples of 2 to 4, and in radial chains with a single fiber separating the vessels; tangential diameter 55–110 μm., mean 83 μm.; radial diameter 60–115 μm., mean 97 μm.; 35–57 per square mm.; length 700–1400 μm.; perforation plates scalariform with more than 20 bars; intervascular pitting opposite to transitional, pits often square or rectangular in outline; vessel–ray pitting similar to intervascular pitting.

Parenchyma. Seen only in longitudinal sections as isolated strands, apparently apotracheal diffuse.

Rays. Multiseriates to 2 (rarely 4) cells wide; 8 to 32 cells, 440–1500 μm. high, markedly heterocellular with 1 to 18 marginal rows of square and upright cells; some rays composite with uniseriate bridges between multiseriate portions of ray; uniseriates 1 to 10 cells, 155–679 μm. high; 8 to 11 per mm.

Imperforate tracheary elements. Pitting not observed.

Material. One specimen of mature secondary xylem.

Holotype. U.S.G.S. Fossil Wood Collection No. D-2054B-41 measuring 34 × 22 × 35 mm.

Locality. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

According to van der Burgh (1964, p. 285), crowded opposite intervascular pits which are somewhat squared in outline are diagnostic of *Nyssa*. This type of pitting occurs in the fossil. The combination of characters of the fossil is diagnostic of the Nyssaceae as determined by a survey of the descriptions of the wood anatomy of different families (Metcalfe & Chalk, 1950). There is also some resemblance to *Ilex*. A few species of *Ilex* do have crowded opposite pits which are square in outline. In most species of *Ilex* there are fewer rows of marginal upright cells, and

the rays are generally wider. One of the characteristics of the fossil is vertical fusion of rays; this feature is found in *Nyssa* (Record & Hess, 1943; and personal observation) and is rare in *Ilex*. Slides of the wood of both *Nyssa* and *Ilex* and the descriptions of *Ilex* species in Baas's (1973) publication were compared with the Yellowstone wood. Wood of *Nyssa javanica* (Hw 16849) and *Nyssa sinensis* (Hw 21459) agrees in every detail with wood of the fossil. Vessel element distribution, density, and size; pitting type; ray structure; and parenchyma distribution are identical.

The genus *Nyssoxylon* was established for those woods resembling *Nyssa* and *Davidia*. *Camptotheca* can be distinguished from these two genera as it has perforation plates with less than 20 bars and very few pore multiples. *Nyssa* and *Davidia* closely resemble one another structurally. Comparing the two genera, Metcalfe and Chalk (1950) found that *Davidia* tends to have a larger number of bars per perforation plate, more scalariform pitting, less parenchyma, a higher ray density, and fibers with more conspicuously bordered pits than *Nyssa*. We examined two slides of *D. involucrata* and found that the vessels were more angular and there were fewer pore multiples than were found in the fossil.

Five species of fossil woods whose affinities are suggested to be with *Nyssa* have been described. These are: *Nyssoxylon japonicum* Mädel (1959) from the Tertiary of Japan; *Nyssa eydei* Prakash & Barghoorn (1961b) from the Miocene of Washington; *Nyssoxylon haanradense* van der Burgh (1964) from the Netherlands brown coal; *N. romanicum* Petrescu (1970) from the Oligocene of Rumania; and *N. ishikariense* Suzuki (1975) from the Eocene of Japan. *Nyssoxylon japonicum* differs from the Yellowstone wood as the former has a higher vessel density, a greater number of bars per perforation plate, and rays only up to two cells wide. *Nyssa eydei* is distinguished from the Yellowstone wood as the former has a lower vessel density, more parenchyma, longer vessel elements, taller rays, a higher ray density, and crystalliferous parenchyma. *Nyssoxylon haanradense* is represented by one poorly preserved specimen, and the features seen in cross section are not described; unlike the Yellowstone wood, however, it does have numerous crystalliferous parenchyma strands and its rays are rarely three cells wide. The most recently described species, *N. ishikariense* Suzuki, has smaller vessels, a higher vessel density, and narrower and more frequent rays than the Yellowstone wood.

Fruits, leaves, and/or pollen of *Nyssa* have been reported from localities in Europe, Asia, and North America ranging in age from Paleocene to Pliocene (Eyde & Barghoorn, 1963). Most of the leaves from North American sites have been compared to the extant species of eastern North America, particularly the *Nyssa sylvatica* complex. Some of the fruits, notably *Nyssa brandoniana* Eyde & Barghoorn (1963) and *Paleonyssa spatulata* Scott (1954), seem more closely to resemble *Nyssa javanica* (Eyde & Barghoorn, 1963). Brown (1962) listed two species of *Nyssa* leaves at a number of Paleocene localities in the Rocky Mountains and

High Plains. A *Nyssa* fruit resembling the extant *N. ogeche* was reported from the Metzel Ranch flora of Montana (Becker, 1972).

At present, *Nyssa* is native to eastern North America and eastern Asia, with *N. sylvatica* occurring in Mexico at altitudes of 3000 to 5000 feet (Eyde, 1963). *Nyssa sinensis* grows in the mixed mesophytic forest and evergreen oak forests of China (Wang, 1961).

Rosaceae

Prunus gummosa (Platen) Wheeler, Scott, & Barghoorn, comb. nov.
Figures 24–27.

Pruninium gummosum Platen, Naturf. Gesell. Leipzig Sitzungsber. **34:** 122–127. 1908.

Growth rings. Present, distinct, 1–7 mm. wide.

Vessel elements. Diffuse porous; solitary, in clusters, or in radial multiples of 2 to 4; tangential diameter 32–74 μm., mean 47 μm.; radial diameter of solitary pores 78–98 μm., mean 90 μm.; length to 370 μm.; spiral thickenings commonly present; perforation plates simple; intervascular pitting alternate, minute to small, pit-pairs round, rarely touching; vessel–ray pits similar to intervascular pitting; tyloses occasionally present.

Parenchyma. Very rare, as isolated strands, generally of 4 cells, seen only in longitudinal sections, apparently apotracheal diffuse.

Rays. Multiseriates to 4 cells wide; 5 to 44 cells, 105–763 μm. high; with uniseriate margins of 1 to 6 (most frequently 1 to 2) rows of square and upright cells; uniseriates 1 to 10 cells, 46–285 μm. high, some composed entirely of square and upright cells, others with some procumbent cells, in tangential section cells of uniseriate rays oval in outline; 8–17 per mm.

Imperforate tracheary elements. Fibers with circular bordered pits on both radial and tangential walls, pits approximately 5 μm. across.

Gum ducts. Traumatic vertical gum ducts present, often in tangential groups at beginning of growth increment.

Material. One specimen, D-2054A-21, of mature secondary xylem, measuring 63 × 71 × 41 mm.

Locality. Amethyst Mountain, U.S.G.S. Paleobot. Loc. No. D-2054A.

The combination of characters of this fossil (small vessels, small to minute alternate intervascular pitting, prominent spiral thickenings, and traumatic vertical canals) is diagnostic of the Rosaceae, exclusive of the Chrysobalanoideae. Pore multiples are characteristic of the Prunoideae (Metcalfe & Chalk, 1950), and *Prunus* is particularly prone to the formation of traumatic vertical canals (Jane, 1970; Panshin & DeZeeuw, 1970; Record & Hess, 1943). As pore multiples and vertical canals are present.

the specimen is assigned to the Prunoideae. Vertical canals also occur in *Laurocerasus* of the Prunoideae, and this genus (a segregate of *Prunus*) is similar anatomically to *Prunus*. *Laurocerasus* may be distinguished from *Prunus* as, in the former, rays frequently have four or more marginal rows and parenchyma is vasicentric (Metcalfe & Chalk, 1950). The Yellowstone wood resembles *Prunus* as it has sparse diffuse parenchyma and generally less than four marginal rows of ray cells.

Pruninium gummosum from Amethyst Mountain was described by Platen in 1908. The differences between his diagnosis and the specimen described here are slight. The quantitative data are nearly identical: according to Platen, maximum tangential diameter is 75 μm., we found it to be 74 μm.; he described rays as up to 50 cells high, we found a maximum height of 44 cells. We did not observe any scalariform perforation plates, although he noted their rare occurrence. The diagnosis of *Pruninium gummosum* is so close to the specimen we studied that it almost seems as if we had fragments from the same stump. There is less variation than may be observed in wood taken from different portions of the same tree. We consider *Pruninium gummosum* Platen and the specimen described here to be conspecific, and their anatomies are indistinguishable from species of the extant genus *Prunus*. As discussed in the first paper on Yellowstone fossil dicotyledonous woods, it is not required that species of fossil wood be assigned to organ genera when their anatomical features are those of a single modern genus and such an assignment obscures the contributions of paleobotany to the history of a genus. Consequently, we hereby transfer the species *Pruninium gummosum* Platen to *Prunus* and make the new combination *Prunus gummosa* (Platen) Wheeler, Scott, & Barghoorn.

Reports of fossil woods of the Rosaceae exclusive of the Chrysobalanoideae are few. *Prunus* (?) (*Beck 1673*) is on a list of woods of the Miocene Vantage fossil forests (Beck, 1945). Thin-sections of this wood (*Beck 1673*, HPC 56667) were examined. This specimen appears to be *Ulmus pacifica* Prakash & Barghoorn (1961a) rather than *Prunus*. There are no other descriptions of fossil wood of the Prunoideae. Fossil woods assigned to the Rosaceae include *Lyonothamnoxylon* Page (1964) from the Pliocene of Nevada, *Rosaceoxylon* Shilkina (1958) from the late Tertiary of Russia, *Maloidoxylon* from the Tertiary of France (Grambast-Fessard, 1966) and the Miocene of Colorado (Wheeler & Matten, 1977), and *Pomoxylon* Hofmann (1944). The last is not a valid name as no species name was assigned nor was a species described when the genus was first named.

Prunus is a cosmopolitan genus of some 430 species (Willis, 1973). Baas (1973) has found that spiral thickenings are characteristic of the temperate members of the genus. Spiral thickenings are prominent in the specimen described here.

Both megafossils and microfossils of *Prunus* occur in the Kisinger Lakes-Tipperary flora. MacGinitie (1974) considered the leaves similar to those of the extant *Prunus serotina* Ehrlich. Species of *Prunus* have also been described from Florissant (MacGinitie, 1953) and the Green River flora

(MacGinitie, 1969), and reported from the older Wind River flora (MacGinitie, 1969).

Staphyleaceae

Turpinia lamarense Wheeler, Scott, & Barghoorn, sp. nov.
Figures 28–32.

Growth rings. Indistinct.

Vessel elements. Solitary and in radial multiples of 2 to 8, mostly 2 to 4; square to rectangular in outline; tangential diameter 55–115 μm., mean 85 μm.; radial diameter 78–155 μm., mean 124 μm.; 14 to 22 per square mm.; length .76–1.47 mm.; perforation plates exclusively scalariform with 26 to 51 bars; intervascular pitting subopposite, opposite, and transitional, often scalariform at ends of vessel elements; vessel–ray pits similar to intervascular pitting.

Parenchyma. Exact distribution not determinable, isolated strands seen in longitudinal section, some adjacent to vessel elements.

Rays. Multiseriates to 4 cells wide, occasionally 5 cells wide; 11 to 37 cells, 415–2440 μm. high; markedly heterocellular with uniseriate margins of up to 16 rows of upright and square cells; vertical ray fusions; uniseriates 2 to 25 cells, 127–1840 μm. high, apparently composed of only square and upright cells; occasionally crystals in slightly enlarged ray cells; 7 to 10 per mm.

Imperforate elements. Some fibers with bordered pits.

Material. One specimen of mature, silicified secondary xylem.

Holotype. U.S.G.S. Fossil Wood Collection No. D-2054B-24, measuring 77 × 27 × 93 mm.

Locality. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

Small vessels that are both solitary and in radial multiples, opposite intervascular pitting, vessel–ray pitting that is round to elongate, exclusively scalariform perforation plates with more than 20 bars, average vessel element length greater than 800 μm., markedly heterocellular rays, and sparse parenchyma are all diagnostic of the Staphyleaceae. The fossil somewhat resembles members of the Styracaceae, but in this family perforation plates generally have fewer than 20 bars, and the vessel–ray pitting is very fine. *Turpinia* is the only genus in the Staphyleaceae with pores in radial multiples and more than ten rows of marginal upright cells, so the fossil is assigned to this genus.

According to Willis (1973), *Turpinia* is a genus comprised of 30 to 40 species occurring from Ceylon to Japan, Malaysia, and Central and tropical South America. We examined only six of the species. The Old World species examined have predominantly solitary vessels, a fairly high vessel

density, thick-walled fibers, and elongate vessel–ray pitting. The New World species examined have numerous radial multiples, a relatively low vessel density, thin-walled fibers, and vessel–ray pits that have a round outline and are not as coarse as those of the Old World species. The structural features of *Turpinia absarokensis* are more consistent with those of the New World species of the genus, at least those available to us for comparison.

The Kisinger Lakes flora (MacGinitie, 1974) does not contain any members of the Staphyleaceae. *Turpinia* appears on a preliminary generic list of the Lost Cabinian Wind River flora of late early Eocene age (MacGinitie, 1969), but we know of no other reports of the genus in the Tertiary of the Rocky Mountains nor of any reports of fossil wood of *Turpinia*. Fossil seeds of *Turpinia* have recently been recognized in the Oligocene Brandon Lignite of Vermont (Tiffney, 1977). The Brandon *Turpinia uliginosa* most closely resembles the New World representatives of the genus. Tiffney based this comparison on the examination of 20 extant species.

ULMACEAE

Zelkovoxylon occidentale Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 33–37.

Growth rings. Distinct.

Vessel elements. Semi-ring porous; transition from earlywood to latewood gradual; tangential diameter of earlywood vessels 83–124 μm., mean 112 μm.; radial diameter 125–190 μm., mean 165 μm.; solitary and in radial multiples of 2 to 4, circular to oval in outline; latewood vessels tangential diameter 36–70 μm., mean 50 μm., in clusters of 3 to 20 cells and more rarely in radial multiples of 2 to 6, often tending to form tangential or oblique bands; perforation plates simple; intervascular pitting crowded alternate, hexagonal in outline due to crowding; spiral thickenings in the smaller elements.

Parenchyma. Paratracheal, vasicentric, or not completely ensheathing vessels or vessel clusters, most commonly 4 cells per strand.

Rays. Multiseriates to 4 (rarely 5) cells wide, 9 to 52 cells, 170–860 μm. high; with 1 to 3 marginal rows of square and upright cells, frequently inflated crystalliferous cells in marginal rows and along side of rays, some homocellular rays also; uniseriate rays few, low, 1 to 4 cells high.

Imperforate tracheary elements. Libriform fibers and vascular tracheids, vascular tracheids with spiral thickenings and crowded alternate pits, generally associated with small vessel elements.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-26, measuring 44 × 34 × 41 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

The structural features of this fossil, particularly latewood pore distribution and spiral thickenings in the smaller tracheary elements, clearly indicate its affinities with the Ulmaceae. Genera in the Ulmaceae with some degree of ring porosity and heterocellular rays are *Celtis*, *Zelkova*, and *Hemiptelea*. *Hemiptelea* is readily distinguishable as it has scalariform perforation plates, few radial multiples, and storied vessels. The Yellowstone wood shares features with both *Zelkova* and *Celtis*. Inflated crystalliferous ray cells are characteristic of *Zelkova*. Ray cells of *Celtis* often contain crystals, but the cells are not enlarged as they are in *Zelkova* and the fossil. Rays in *Celtis* are predominantly heterocellular; those in *Zelkova* are predominantly homocellular. Wood of extant *Zelkova* species is strictly ring porous, the transition from earlywood to latewood is very abrupt, and there is a distinct band of large earlywood pores. Radial multiples are very rare in *Zelkova*, occurring in only 0 to 8 percent of the pores (Sweitzer, 1971).

Celtis is an anatomically diverse genus with both diffuse and ring porous species. The abruptness of the transition from earlywood to latewood may vary within a species, probably reflecting differences in habitat. Five of six specimens of *C. occidentalis* had an abrupt transition from earlywood to latewood, while one was semi-ring porous with a gradual transition in size and distribution of the pores. Sweitzer (1971) studied three specimens of *Planera*: two were diffuse porous, the third ring porous. The arrangement of the pores, in addition to the size, differs between ring and diffuse porous species: radial multiples are common in the diffuse porous species of *Celtis*, rare in ring porous species.

Sweitzer (1971) suggested that ring porosity and spirals should be considered as specializations in Ulmaceae which are correlated with a seasonal temperate environment. Cox (1941) studied species of *Celtis* from temperate and tropical regions and concluded that species of tropical zones are diffuse porous and lack spiral thickenings, while those of temperate regions are ring porous and have spiral thickenings. Spiral thickenings are present in the small tracheary elements of the Yellowstone fossil and it is intermediate in the development of the ring porous condition.

The earliest known ring porous woods are Eocene (Chowdhury, 1964). The known early Eocene floras of North America indicate that rainfall was evenly distributed throughout the year. MacGinitie (1974) suggested that by the early middle Eocene, the climate of the Rocky Mountains was seasonal. The development of ring porosity may be correlated with the advent of a seasonal climate.

The fossil wood described here resembles *Celtis* as both have similar pore distribution, but the fossil wood has a character (inflated ray cells) that occurs only in *Zelkova*, a genus with ring porous wood.

Celtis is not common in the fossil record of the Rocky Mountains, while *Zelkova* is common. *Celtis mccoshii* Lesquereux is one of the least common fossils in the Eocene Green River flora and is also rare in the Oligocene Florissant flora (MacGinitie, 1969, 1953). *Zelkova* is a member of the Kisinger Lakes flora (MacGinitie, 1974). One may speculate that this

wood might represent wood of a tree which had foliage recognizable as *Zelkova*, but whose wood had not yet developed the presumably derived ring porous condition. The wood does share more features with *Celtis* than with *Zelkova*, and it is difficult to assess how much weight should be attached to a single distinctive feature, such as these enlarged ray cells.

A fossil wood that is very similar to the Yellowstone wood is *Zelkovoxylon dacicum* Petrescu (1971) from the Oligocene of Rumania. It has very inflated crystalliferous ray cells, like extant *Zelkova* and the Yellowstone specimen. It also has vessels in radial multiples, heterocellular rays, and is semi-ring porous, all features present in the Yellowstone wood, but which neither Sweitzer nor we found to be characteristic of *Zelkova*. Petrescu seems to have weighted the one character, inflated crystalliferous cells, in determining the affinities of the Rumanian wood.

We do not consider the Yellowstone wood to be structurally equivalent to extant *Zelkova*, but for the three reasons listed below we name it a species of *Zelkovoxylon*, implying some, but not complete, resemblance to extant *Zelkova*. First, ring porosity in the Ulmaceae is, at times, under environmental control, and pore distribution is affected by the degree to which the ring porous condition is expressed. Pore distribution is variable within a genus because of this. Second, the Yellowstone wood has inflated crystalliferous ray cells, a feature unique to *Zelkova*. Third, there is a precedent for assigning the name *Zelkovoxylon* to woods with the combination of features found in the fossil.

There are three species of fossil wood which are very similar to *Zelkova*, as they are ring porous with a narrow, well-defined earlywood pore zone. These are *Zelkova zelkoviformis* (Watari) Watari (1941, 1952) and *Z. wakimizui* (Watari) Watari (1948, 1952) from the Miocene of Japan, and *Zelkovoxylon yatsenkokhmelvskyi* Greguss (1969) from the Miocene of Hungary. All three are younger than the two semi-ring porous species of *Zelkovoxylon*.

At present, the genus *Zelkova* is comprised of six or seven species which are distributed in the eastern Mediterranean, the Caucasus, and eastern Asia (Willis, 1973).

DISCUSSION

The ten species of fossil wood described in this paper represent a combination of so-called temperate and paratropical forms, as do the eight species described in our first paper (Wheeler, Scott, & Barghoorn, 1977). Two of the woods, *Cyrilloxylon eocenicum* and *Prunus gummosa*, have structural features (semi-ring porosity and spiral thickenings, respectively) which are generally found in the extant representatives that grow at higher latitudes. In contrast, *Turpinia lamarense* has indistinct growth rings, a character considered to be indicative of more tropical conditions.

Zelkovoxylon occidentale, a wood that is intermediate in structure between two well-defined extant genera (*Zelkova* and *Celtis*), differs from the present-day *Zelkova* in degree of ring porosity and pore distribution, the

latter a feature affected by the degree of ring porosity. The ring porous condition in the Ulmaceae is believed to be a specialization developed in response to a seasonal temperate environment. The absence of ring porosity in this specimen may reflect the absence of such an environment. This is consistent with the subtropical climatic conditions already inferred for the Yellowstone fossil forests (Dorf, 1960, 1964) and the near-tropical climate of the nearby Kisinger Lakes flora of similar age to the Yellowstone flora (MacGinitie, 1974).

MacGinitie (1974) has commented on the lack of similarity of the Yellowstone leaf and Kisinger Lakes floras. The Kisinger Lakes flora is approximately 80 miles southeast of the Yellowstone flora, and the two are of similar age. The Kisinger Lakes flora has a "distinct tropical American aspect" and is apparently unlike the older, early Eocene floras of the Rocky Mountains which appear to have relationships to the evergreen broad-leaved and mixed mesophytic forest types. In contrast, the Yellowstone fossil flora, as presently known, does not appear to have a strong relationship to the Neotropics. None of the 18 species of wood we have described to date indicates such affinities, and many (*Quercinium*, *Pterocaryoxylon*, *Myrica*, *Nyssa*, and *Prunus*) are related to extant genera which grow in the evergreen sclerophyllous broad-leaved and/or the mixed mesophytic forest types. More detailed comparison of the Yellowstone flora with other Tertiary floras of the Rocky Mountains will be reserved for our third and final paper.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1–3. *Rhus crystallifera*, sp. nov.: 1, transverse section, × 40; 2, intervascular pitting, × 200; 3, tangential section showing septate fibers and rays with crystalliferous cells, × 50. FIGURES 4–7. *Cyrilloxylon eocenicum*, sp. nov.: 4, transverse section, × 45; 5, scalariform perforation plate, × 140; 6, opposite and scalariform intervascular pitting, × 140; 7, tangential section, × 60. FIGURE 8. *Quercinium amethystianum*, sp. nov.: transverse section, note abundant parenchyma, × 16.

PLATE II

FIGURE 9. *Quercinium amethystianum*, sp. nov.: transverse section, × 50. FIGURES 10–12. *Quercinium lamarense* Knowlton, emend. Wheeler, Scott, & Barghoorn: 10, transverse section, growth ring boundary, D-2054B-42, × 50; 11, transverse section, type specimen, × 16; 12, transverse section, D-2054B-42, × 16. FIGURES 13–15. *Pterocaryoxylon knowltonii*, sp. nov.: 13, transverse section showing diagonal pore arrangement, × 25; 14, intervascular pitting, × 200; 15, tangential section, note three-seriate rays, × 120.

PLATE III

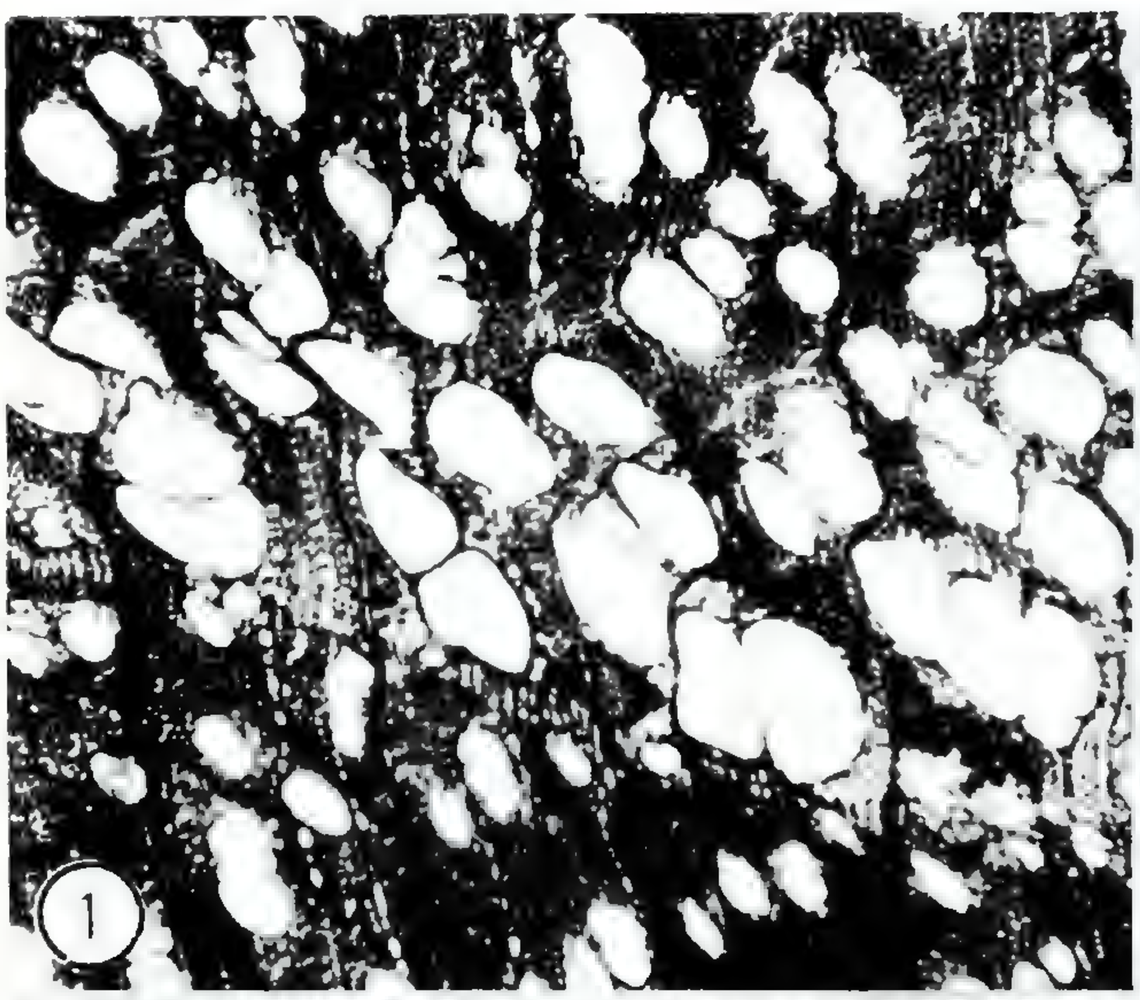
FIGURES 16–19. *Myrica absarokensis*, sp. nov.: 16, transverse section, × 80; 17, tangential section, note crystalliferous parenchyma strands, × 120; 18, scalariform perforation plate, × 300; 19, vessel to ray parenchyma pitting, × 300. FIGURES 20–23. *Nyssoxylon saximontanum*, sp. nov.: 20, transverse section, × 50; 21, opposite-transitional intervascular pitting, × 220; 22, scalariform perforation plate, × 375; 23, tangential section, note composite rays, × 100. FIGURE 24. *Prunus gummosa*, comb. nov.: tangential section, × 80.

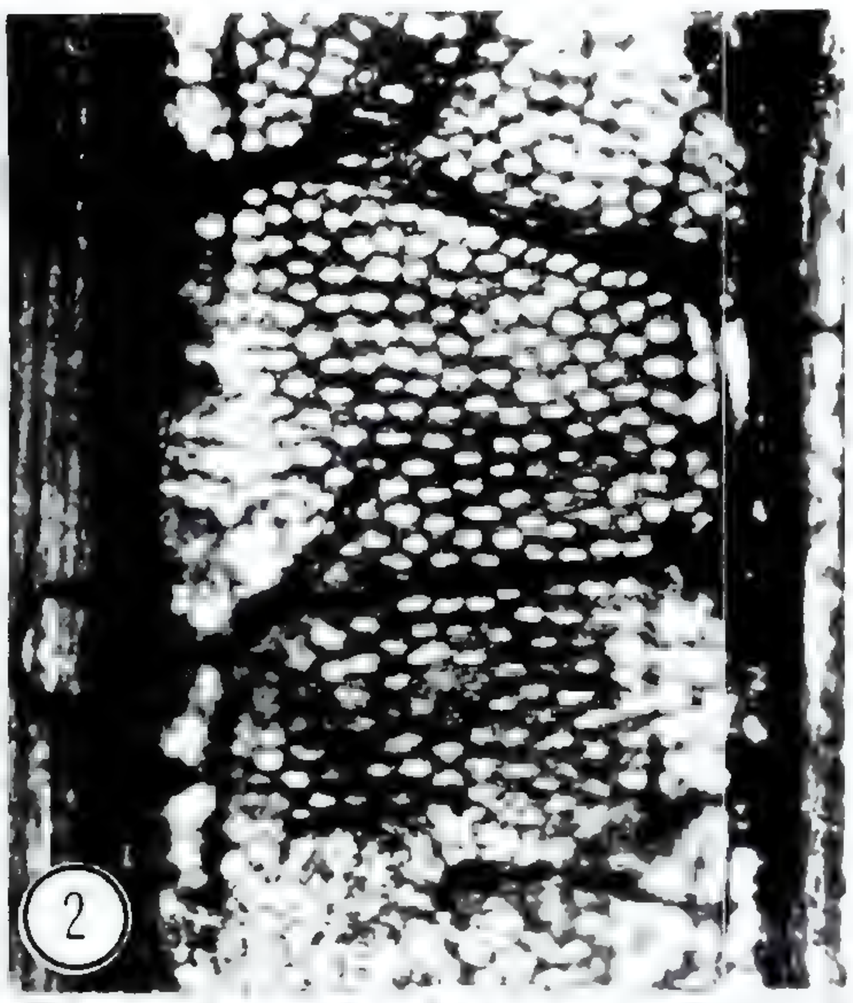
PLATE IV

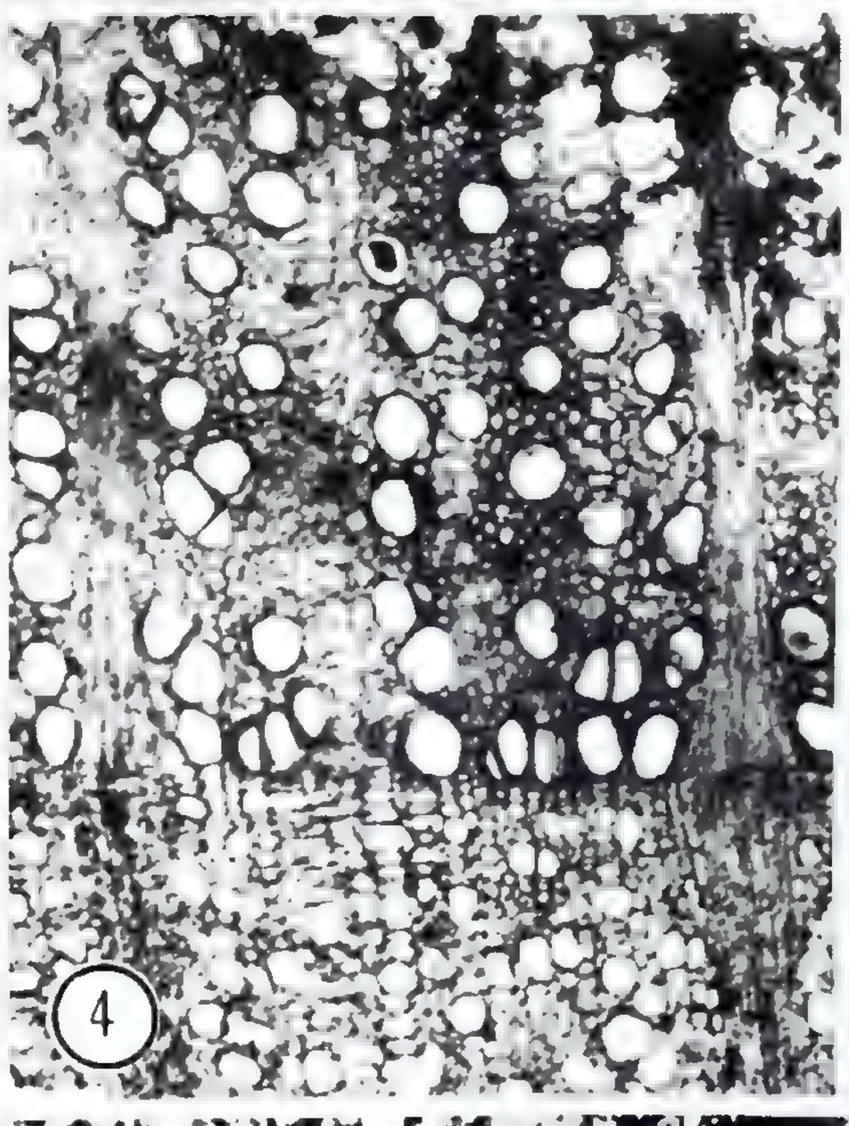
FIGURES 25–27. *Prunus gummosa*, comb. nov.: 25, transverse section showing traumatic gum canals, × 40; 26, spiral thickenings in small vessel element, × 100; 27, simple perforation plate and vessel to ray parenchyma pitting, × 220. FIGURES 28–32. *Turpinia lamarense*, sp. nov.: 28, transverse section, × 60; 29, tangential section, × 50; 30, opposite intervascular pitting, × 300; 31, scalariform perforation plate, × 220; 32, vessel to ray parenchyma pitting, × 220.

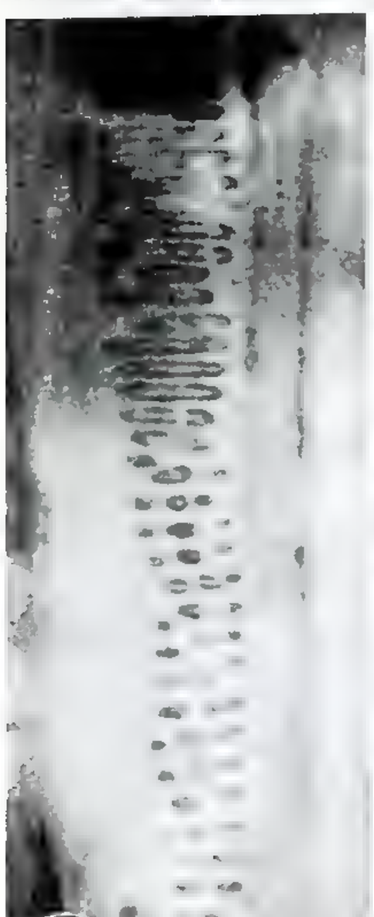
PLATE V

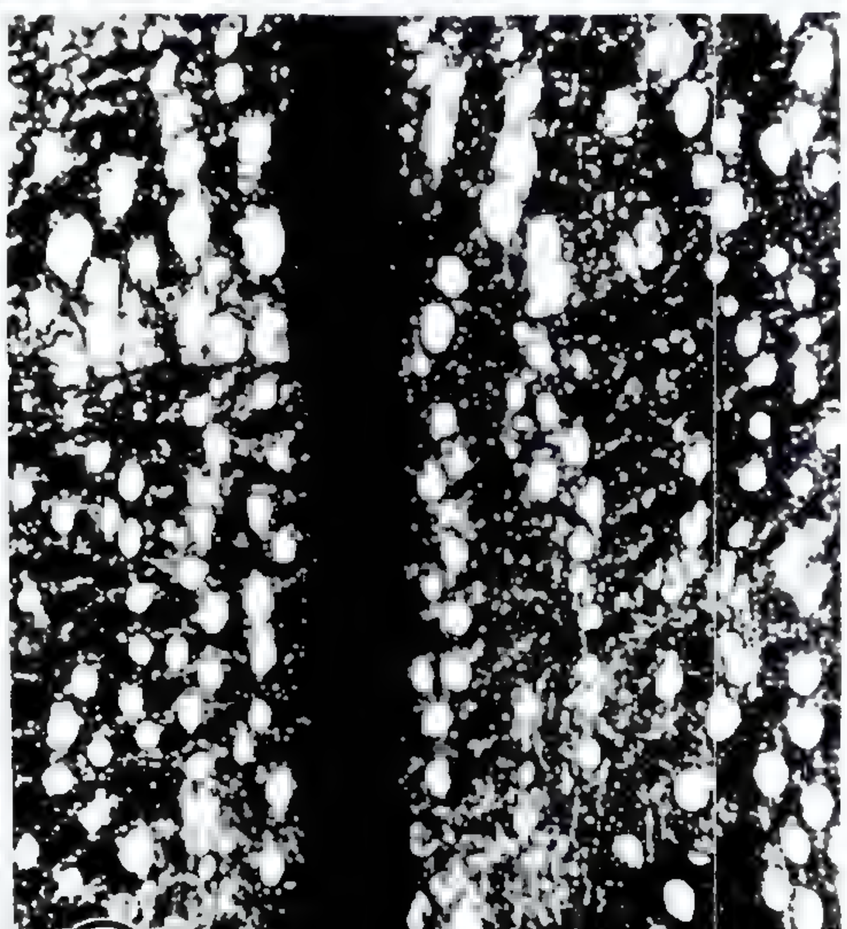
FIGURES 33–37. *Zelkovoxylon occidentale*, sp. nov.: 33, transverse section, note semi-ring porous condition, × 40; 34, simple perforation plate, × 150; 35, spiral thickening in small tracheary element, × 150; 36, tangential section, × 50; 37, tangential section showing crystalliferous marginal ray cell, × 180.



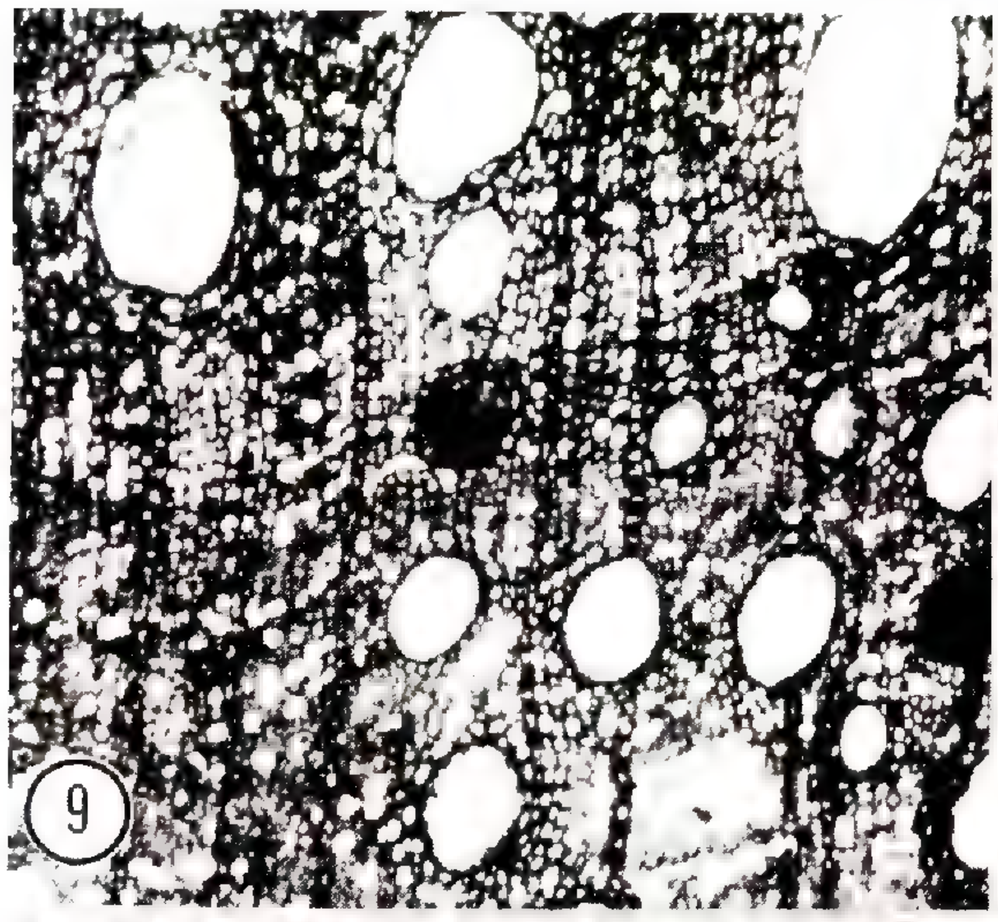








WHEELER ET AL., FOSSIL WOODS, II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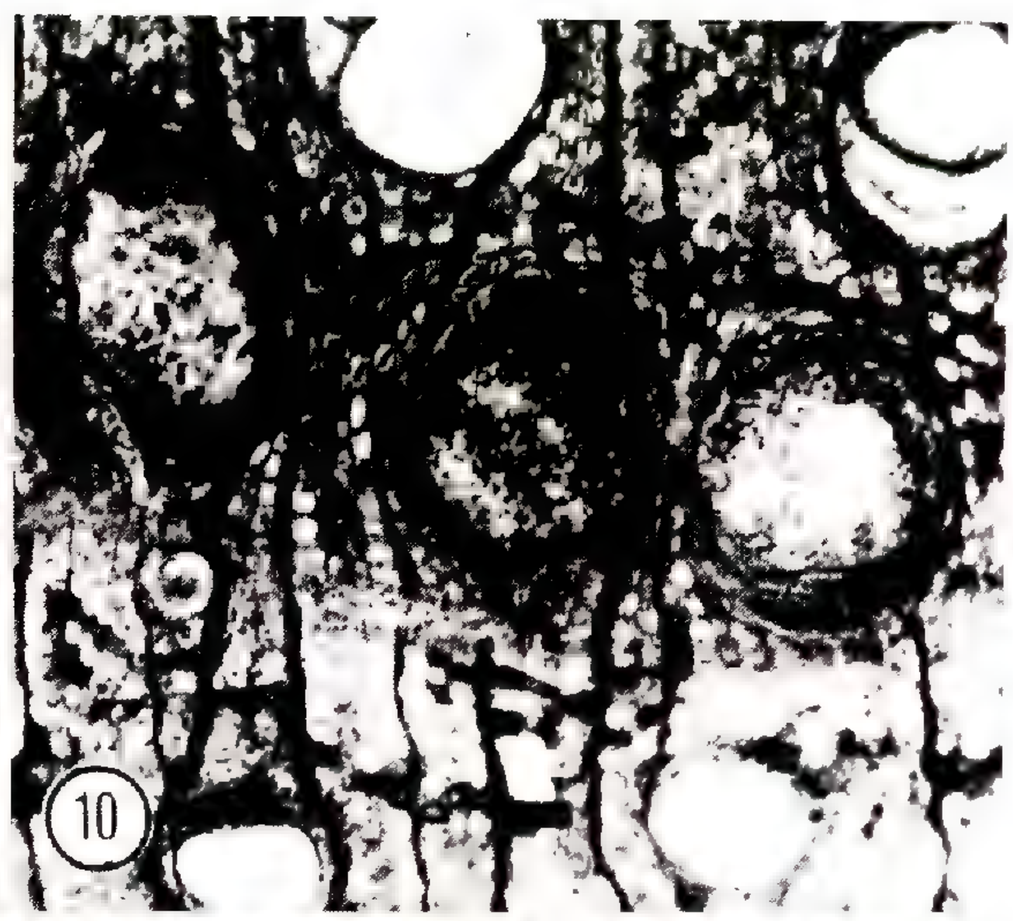
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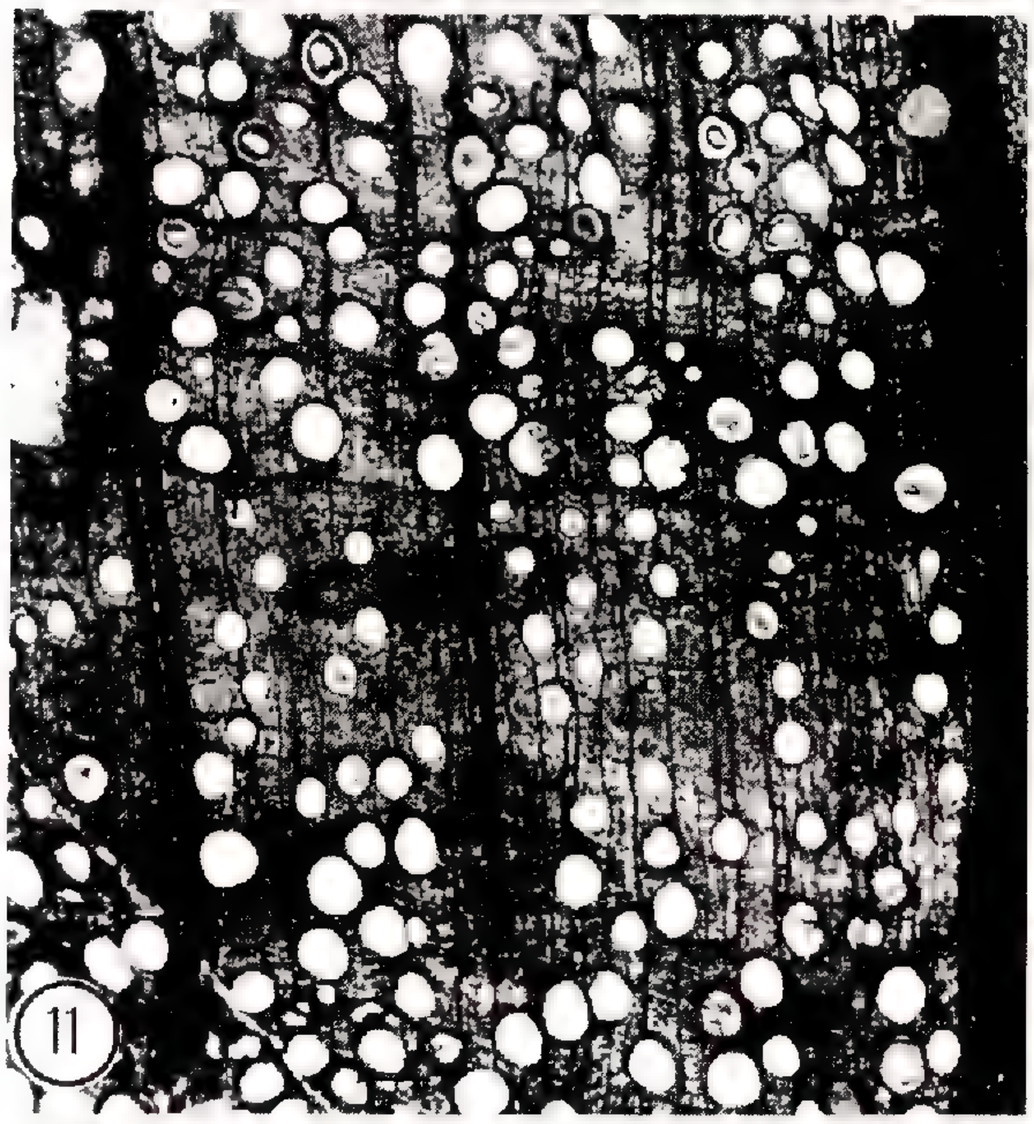
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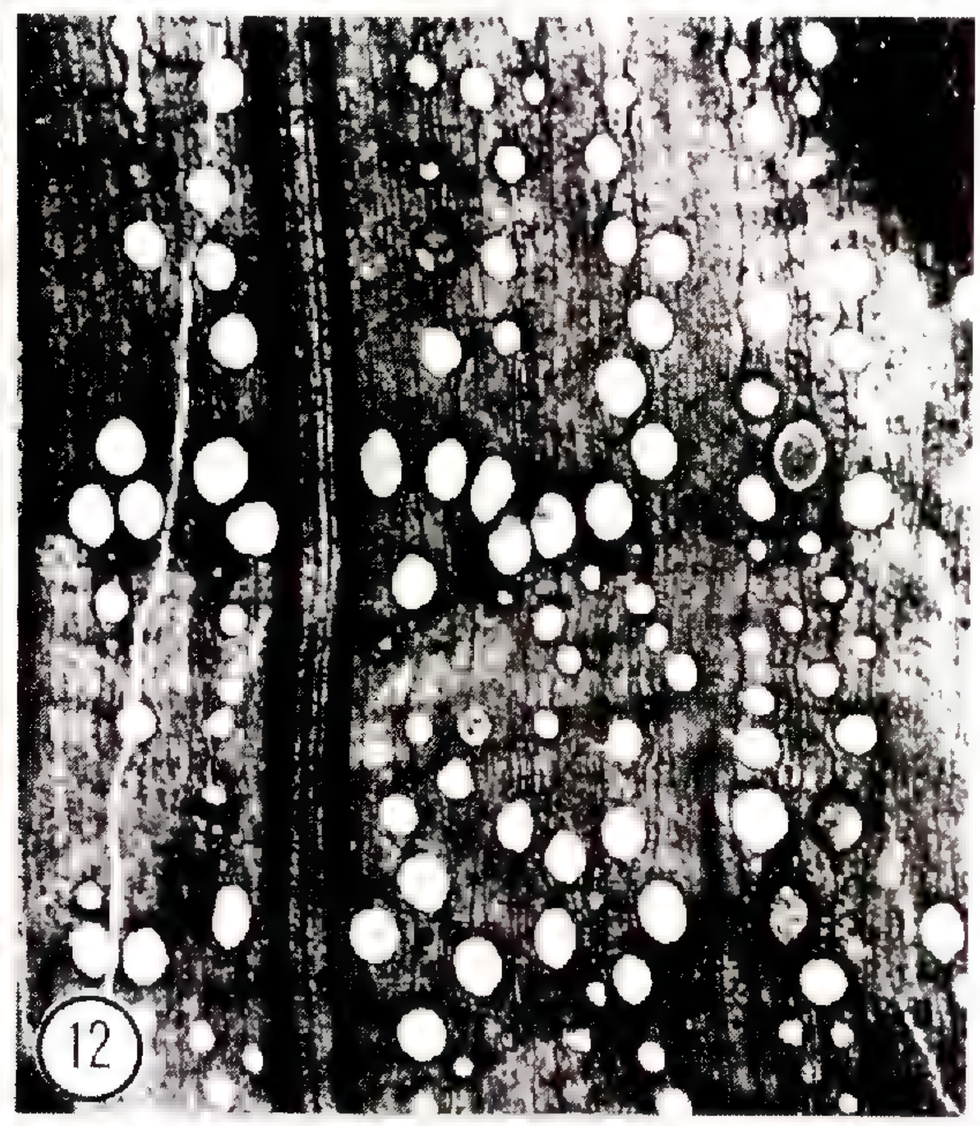
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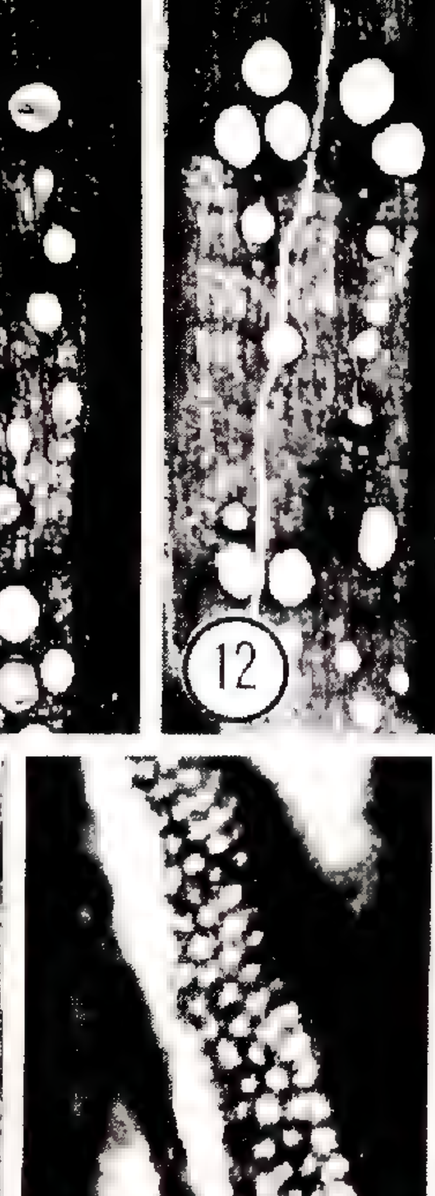
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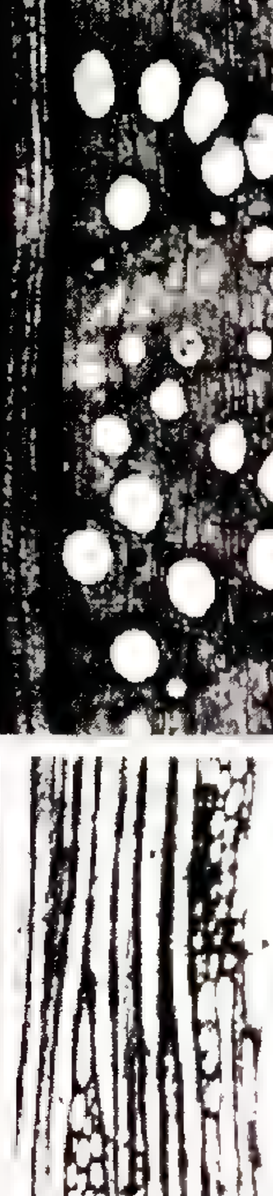
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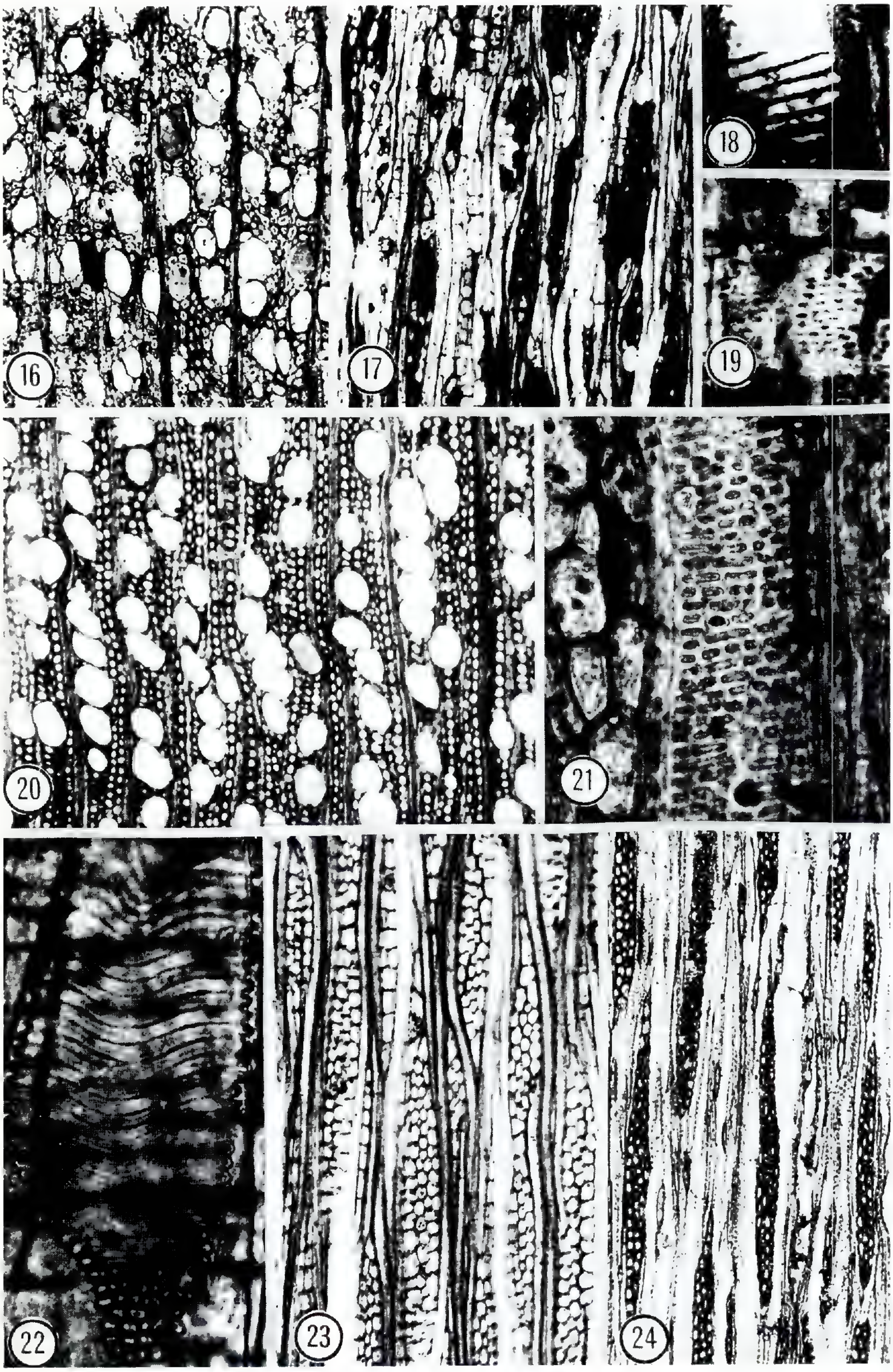

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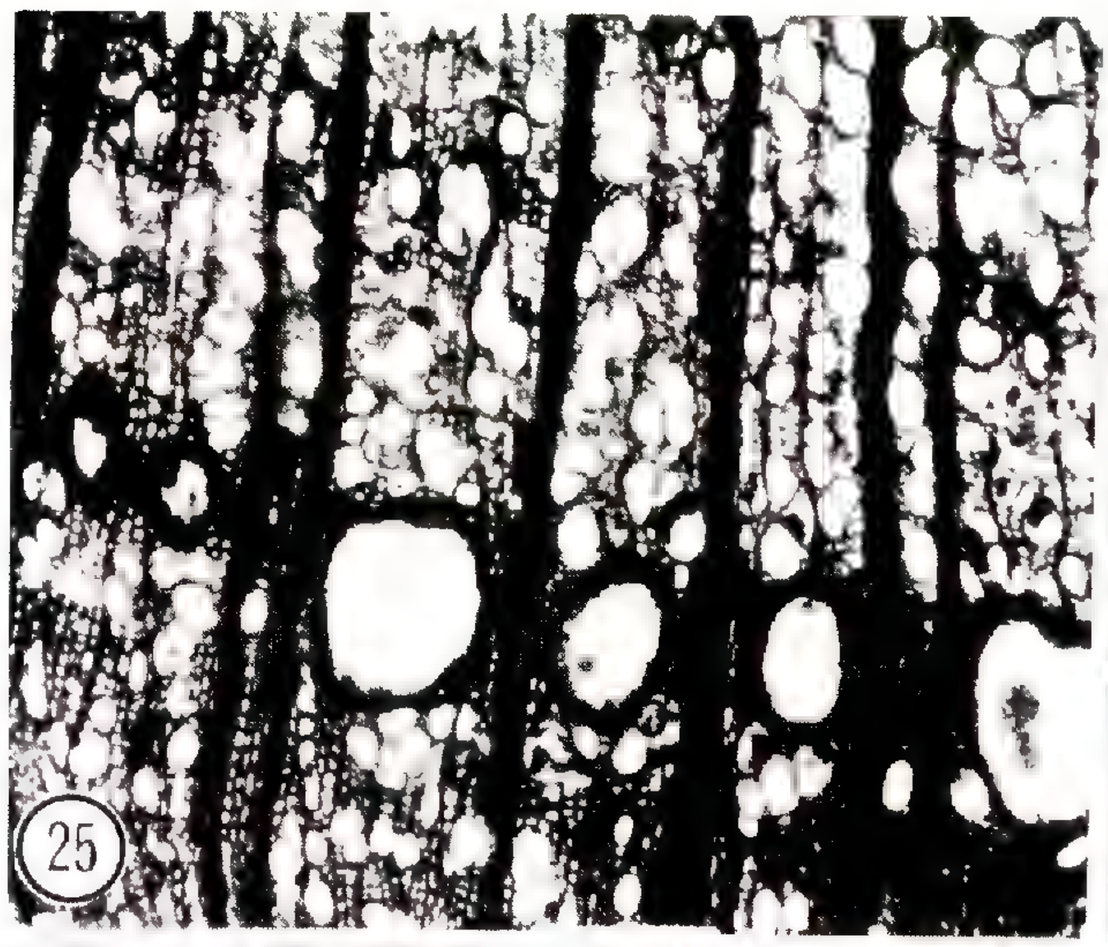
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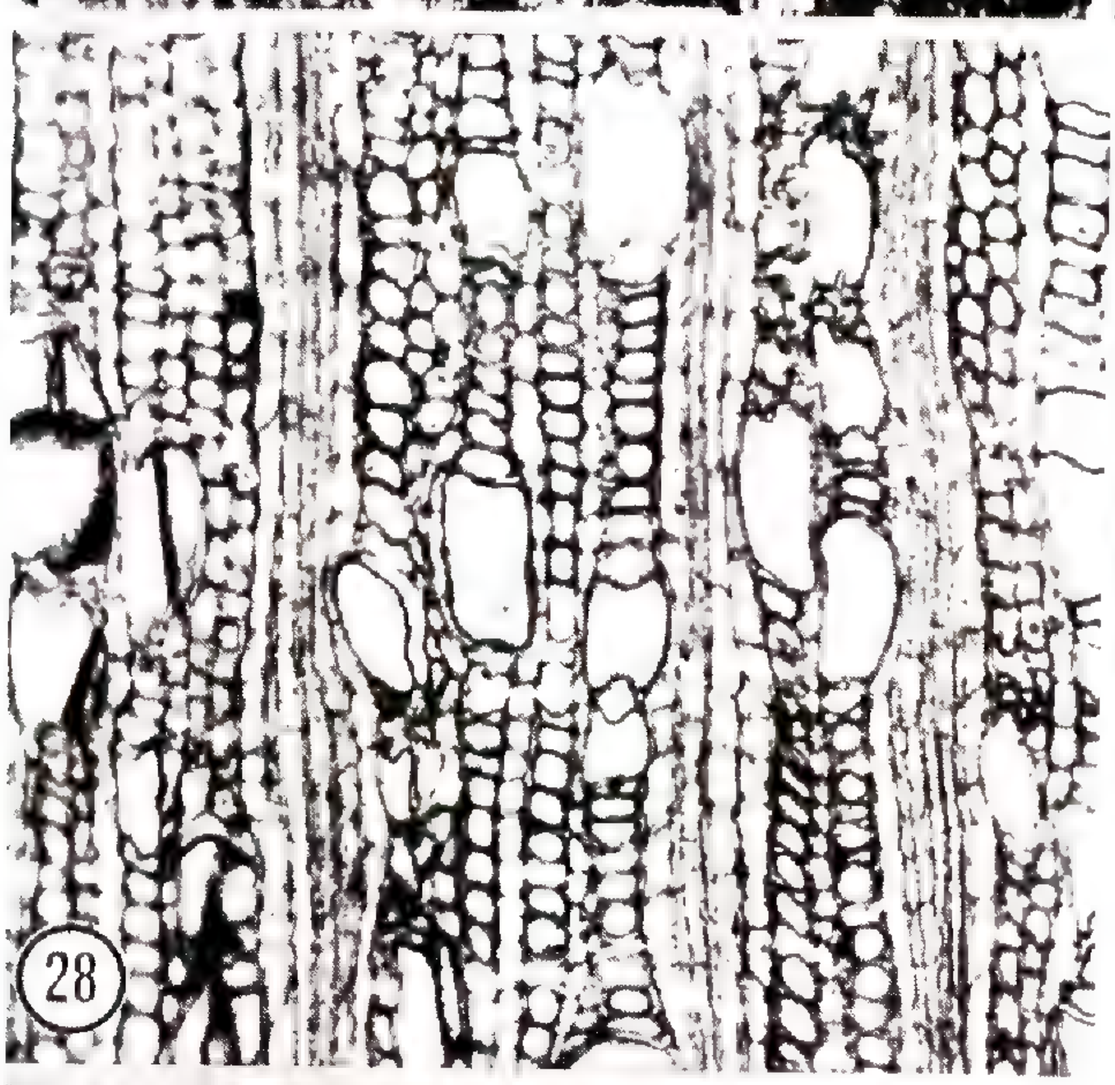
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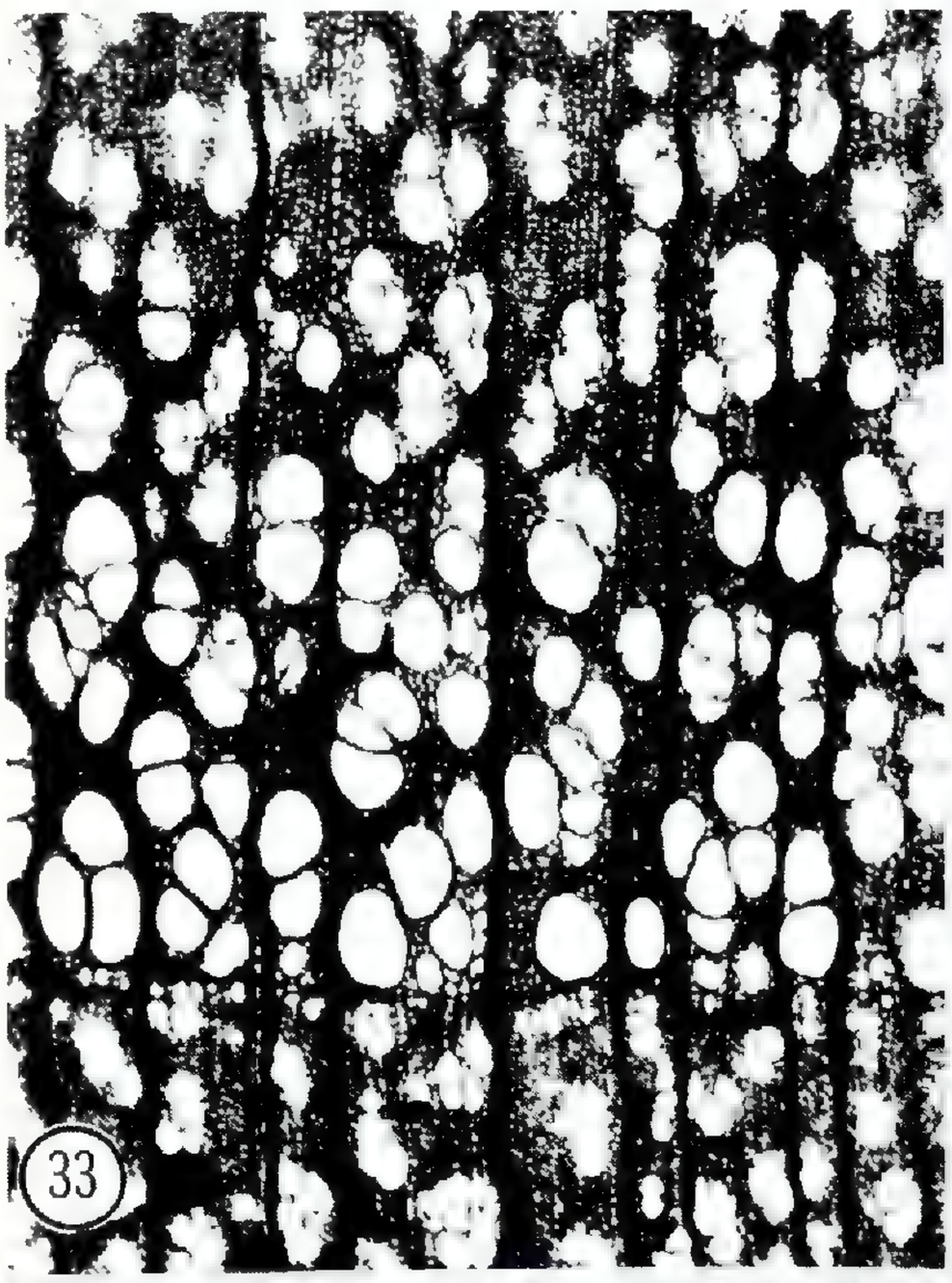
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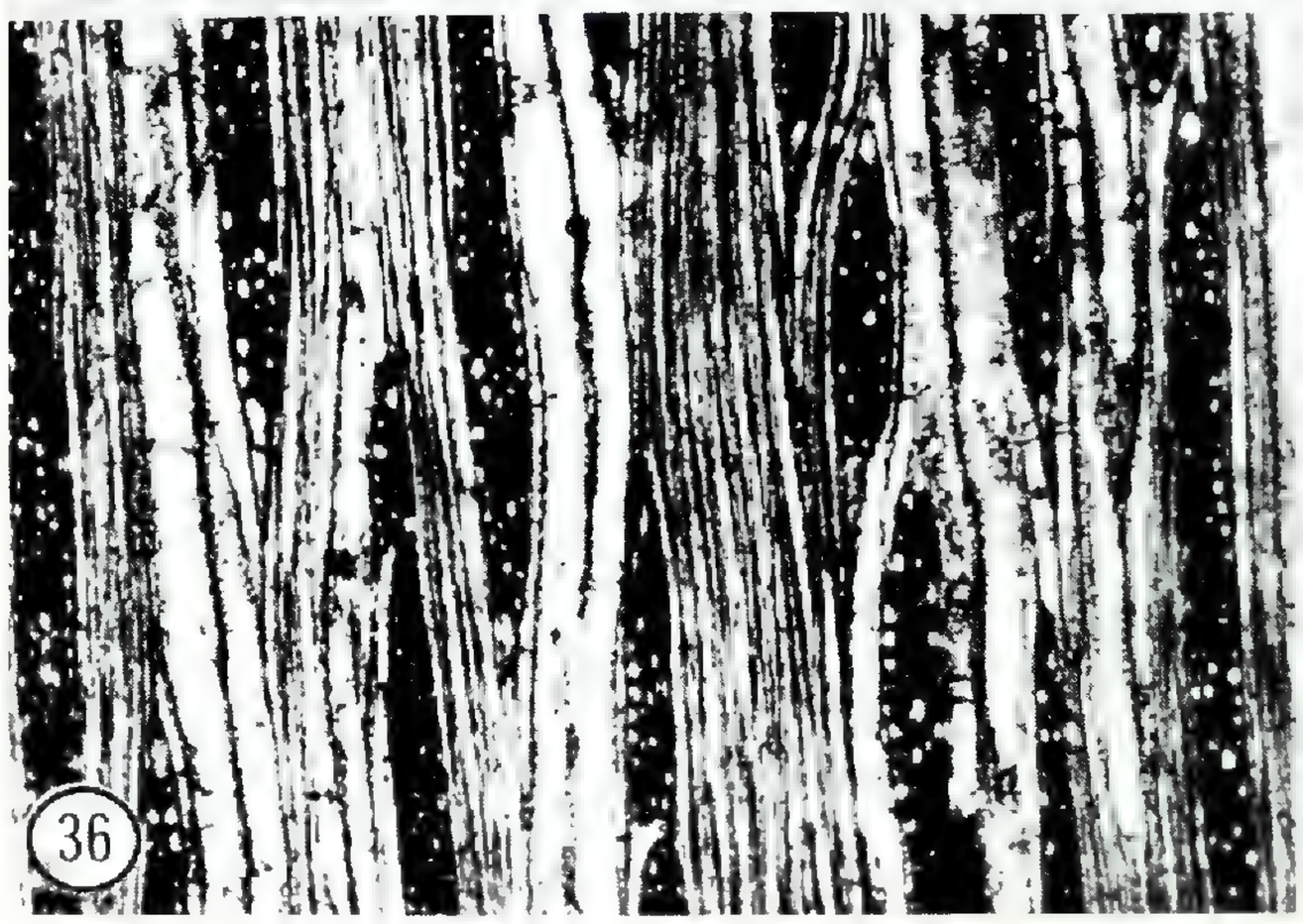
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XYLEM ANATOMY OF HIBBERTIA (DILLENIACEAE) IN RELATION TO ECOLOGY AND EVOLUTION

WILLIAM C. DICKISON, PHILLIP M. RURY, AND
G. LEDYARD STEBBINS

IN A RECENT REVIEW of xylem anatomy, Carlquist (1975) quoted a statement by Bailey (1966), stressing the importance of relating wood anatomical diversity to ecological and physiological influences in habitats where the plants normally grow, and suggested that such relations are best established by comparing species within a genus. A preliminary comparison of this kind is here presented for the genus *Hibbertia* Andr., which contains about 150 species of shrubs, small trees, or vines that occur primarily in Australia and New Caledonia. As pointed out by Stebbins and Hoogland (1976), *Hibbertia* includes an extraordinarily wide range of diversity with respect to growth habit, size and structure of leaves, floral morphology, chromosome numbers, and ecological adaptations. Furthermore, the least specialized members of the genus are in many ways among the least specialized of modern angiosperms with respect to the majority of their morphological characteristics (Stebbins, 1974). The primitive condition of *Hibbertia* xylem in comparison to that of other Dilleniaceae was recognized by Dickison (1967). A thorough analysis of variation in venation patterns of the leaves (Rury & Dickison, 1977) has shown that foliar venation is rather generalized in some species, but highly specialized in others, and that species having relatively specialized floral structures usually have more specialized leaf morphologies. The data reported in this paper can, accordingly, be discussed within the context of the wide morphological and ecological variation present within the genus, and the family Dilleniaceae as a whole.

MATERIALS AND METHODS

Woods of 27 species of *Hibbertia* were studied. Sources of specimens and other pertinent collecting data are presented in TABLE 1. Wood samples were boiled in water and cut on a sledge microtome at a thickness of 20 to 30 μm. Smaller stems were initially glued onto wood blocks prior to sectioning. Resulting sections were stained with safranin. Data relating to wood cell length were obtained by making at least 25 measurements from macerations prepared using Jeffrey's solution. Vessel elements were measured from tip to tip. Cell diameters were measured from transverse sections. Wood terminology follows the *Multilingual Glossary of Terms used in Wood Anatomy* (Committee on Nomenclature, International Association of Wood Anatomists, 1964). For the most part, categories of measurement follow the suggestions of the Committee on Standardization of Terms of Cell Size (1937, 1939).

TABLE 1. **Wood specimens of Hibbertia examined.**

SPECIES	COLLECTOR	COLLECTION LOCALITY	HERBARIUM VOUCHER [a]	XYLARIUM
altigena Schltr.	*H. S. MacKee 3549*	New Caledonia	L	—
aspera DC.	*P. G. Wilson 680*	S. Australia	L	—
banksii Bentham	*L. J. Brass 8431*	Papua	L	—
baudouinii Brongn. & Gris	?	New Caledonia	?	BRIw 13033
baudouinii Brongn. & Gris	*H. S. MacKee 3818*	New Caledonia	L	—
coriacea (Pers.) Baillon	*Lam & Meeuse 6068*	Madagascar	L	—
cuneiformis (Labill.) Sm.	?	W. Australia	?	BRIw 11684
cuneiformis (Labill.) Sm.	*Carlquist 1017*	W. Australia	RSA	RSAw
cuneiformis (Labill.) Sm.	*Carlquist 6085*	W. Australia	RSA	RSAw
drummondii (Turcz.) Gilg	*Stebbins & Keighery A–25*	W. Australia	UCB	—
exutiacies N. A. Wakefield	*Kraehenbuehl 2153*	S. Australia	NCU	—
furfuracea (DC.) Bentham	*Carlquist 6056*	W. Australia	RSA	RSAw
glaberrima F. Mueller	*D. J. Whibley 1081*	S. Australia	NCU	—
huegelii (Endl.) F. Mueller	*E. Pritzel 572*	Australia	L	—
huegelii (Endl.) F. Mueller	*Stebbins & Keighery A–9*	Australia	UCB	—
hypericoides (DC.) Bentham	*A. Morrison s.n.*	W. Australia	L	—
lineata Steudel	*Carlquist 5940*	Australia	RSA	RSAw
lucens Brongn. & Gris	*A. C. Smith 3546*	Fiji	MAD, NY	SJRw 28402
lucens Brongn. & Gris	*A. C. Smith 3045*	Fiji	MAD, NY	SJRw 27903
lucens Brongn. & Gris	?	New Caledonia	?	BRIw 12037

TABLE 1. **Wood specimens of Hibbertia examined** (*continued*).

SPECIES	COLLECTOR	COLLECTION LOCALITY	HERBARIUM VOUCHER [a]	XYLARIUM
montana Steudel	*Stebbins & Keighery A–38*	Australia	UCB	—
ngoyensis Schltr.	*H. S. MacKee 32303*	New Caledonia	NCU	NCU
obtusifolia DC.	*G. L. Stebbins A–53*	A.C.T., Australia	UCB	—
obtusifolia DC.	*Hoogland 3067*	A.C.T., Australia	L	—
potentilliflora Bentham	*Stebbins & Keighery*	W. Australia	UCB	—
procumbens (Labill.) DC.	*N. T. Burbidge 3326*	Tasmania	L	—
saligna DC.	?	N.S.W., Australia	?	BRIw 13034
saligna DC.	*E. F. Constable 4434*	N.S.W., Australia	NCU	—
scandens (Willd.) Gilg	*R. D. Hoogland 3115*	Queensland, Australia	L	—
scandens (Willd.) Gilg	—	Cult. BRI s.n.	—	—
sericea (DC.) Bentham	*E. F. Constable 3850*	N.S.W., Australia	NCU	—
sericea (DC.) Bentham	*M. C. R. Sharrad 342*	S. Australia	L	—
serrata Hotchkiss	*C. L. Wilson 855*	Australia	US	—
stricta (DC.) F. Mueller	*D. J. Whibley 855*	S. Australia	NCU	—
trachyphylla Schltr.	?	New Caledonia	L	—
uncinata (Bentham) F. Mueller	*Stebbins & Keighery A–3*	Australia	UCB	—
virgata R. Br. ex DC.	*B. J. Blaylock 575*	S. Australia	NCU	—

[a] Abbreviations follow Holmgren and Keuken (1974) in *Index Herbariorum*.

OBSERVATIONS

GROWTH RINGS. Well-defined growth rings are recognizable by the presence of thicker-walled imperforate tracheary elements in the late wood of the Australian species *Hibbertia drummondii*, *H. huegelii*, *H. montana*, *H. exutiacies*, *H. virgata*, *H. potentilliflora*, *H. saligna*, *H. stricta*, *H. uncinata*, *H. hypericoides*, and *H. obtusifolia*. Very weak growth rings are also evident in *H. cuneiformis* and *H. sericea*. Growth rings are irregularly spaced and conspicuously wavy in outline as viewed in transection. Woods of *H. exutiacies* and *H. virgata* are, in addition, distinctly ring porous, as shown by the restriction of larger vessel elements to the early wood of a growth ring.

VESSEL ELEMENTS. Selected characteristics of the wood of species studied are summarized in TABLE 2. Four species, *Hibbertia lucens*, *H. saligna*, *H. cuneiformis*, and *H. coriacea*, formed the basis of the description of *Hibbertia* wood by Dickison (1967). In spite of the fact that they belong to different sections of the genus (which in floral morphology differ from each other so much that they might best be regarded as subgenera), these species are very similar to each other with respect to xylem structure. Wood of the remaining species is here recorded for the first time and reveals an interesting diversity of anatomical structure previously unreported for the genus *Hibbertia*.

In most plants the shape of the pores varies from slightly angular to circular. In *Hibbertia saligna*, *H. lucens*, *H. cuneiformis*, *H. trachyphylla*, and *H. obtusifolia* the pores are decidedly angular, whereas in *H. scandens*, *H. huegelii*, and *H. exutiacies* there is a strong tendency toward a circular outline. As reported by Dickison (*loc. cit.*), vessel elements are solitary in distribution; the paired condition is present only in the region of vessel element overlap. Walls are typically of medium thickness, but decidedly thin-walled vessels occur in the Australian *H. scandens* and in *H. ngoyensis* of New Caledonia. Vessel walls of the other New Caledonian plants examined also show a tendency toward the thin-walled condition. Mean pore diameters range from extremely small in the low, shrubby species to mostly moderately small in the larger tree forms. In the single collection of *H. hypericoides* studied, pores have extremely small diameters, making it difficult to distinguish vessels from imperforate tracheary elements in transection. Vessel diameter in *H. scandens* has clearly increased in response to the liana habit. The number of pores per unit area varies considerably, being highest in *H. stricta* and *H. exutiacies*, and lowest in *H. scandens*. Within the genus, mean vessel element length ranges between medium sized and moderately long.

Intervessel pitting is sparse, but where present is opposite to transitional to scalariform in distribution. Pits are circular to scalariform in outline and range in size from minute to very large. Ray–vessel pitting is half-bordered with a distribution pattern similar to that of intervessel pitting. *Hibbertia procumbens*, a prostrate semi-xeric species from southeastern

TABLE 2. **Summary of selected wood anatomical features of Hibbertia in relation to growth habit and habitat.**

(Data from immature samples are in parentheses.) The numbers corresponding to character states are: 1, number of samples studied; 2, geographical distribution; 3, ecological preferences; 4, growth habit; 5, leaf size; 6, diameter of stems studied; 7, growth rings; 8, range in vessel element length, μm.; 9, mean vessel element length, μm.; 10, mean vessel diameter, μm.; 11, perforation plates scalariform only; 12, perforation plates scalariform and simple; 13, bars per scalariform perforation, average; 14, mean fiber length, μm.; 15, fiber wall thickness.

Section and species	1	2	3[a]	4	5[b]	6[c]	7[d]	8	9	10	11	12	13	14	15[e]
Polystiche															
baudouinii	2	New Caledonia	M	rosette tree, 10 m.	L. S. 4	M	-	660-1408	1078	57	+		17	1441	m, t
Spicatae															
ngoyensis	1	New Caledonia	M	rosette tree, 6 m.	L. S. 3	M	-	759-1243	968	95	+		22	1804	t
lucens	3	New Caledonia, Fiji	SX	shrub or rosette tree	L. S. 3	M	-	625-2037	1074	61	+		42	1551	m, t
trachyphylla	1	New Caledonia	SX	shrub or rosette tree	L. S. 3	6.0 mm.	-	(418-1034)	(726)	(40)	+		(24)	(1056)	m, t
altigena	1	New Caledonia	SX	shrub, 1.0 m.	L. S. 2	4.0 mm.	±	(341-1012)	(682)	(35)	+		(32)	(1001)	m
Cyclandra															
saligna	2	E. Australia, N.S.W.	M	erect shrub, 60-90 cm.	L. S. 3	M	+	770-1694	1199	38	+		46	1351	m, t
serrata	1	S.W. Australia	M	shrub, 2-3 m.	L. S. 3	?[f]	?	?	979	?	+		32	1133	?
obtusifolia	2	S.E. Australia	SX	small, erect shrub, 0.1 m.	L. S. 3	4.0 mm.	+	308-957	627	25	+		17	825	m
scandens	2	E. Australia	M	vine	L. S. 3	8 mm.	-	413-1430	731	45	+		9	943	t

montana	1	W. Australia	SX	shrub, 0.5-1.5 m.	L. S. 2	2.0 mm.	+	440-990	651	14	+	8	747	m
drummondii	1	Interior of W. Australia	X	shrub, 0.5 m.	L. S. 2	2.5 mm.	+	220-880	513	13	+	2	803	th
glaberrima	1	Interior of S. & N. Australia	SX-X	shrub	L. S. 2-L. S. 3	4.0 mm.	-	220-825	497	23	+	3	760	m, th
potentilliflora	1	W. Australia	SX	semi-prostrate shrub	L. S. 3	4.1 mm.	+	270-622	411	15	+	4	551	m
virgata	1	E. Australia	SX	shrub, 0.5 m.	L. S. 1	3.5 mm.	+	248-550	400	14	+	8	584	m, t
procumbens	1	Tasmania, E. Australia	SX	prostrate shrub	L. S. 1-L. S. 2	-	?	165-671	451	?	+	28	517	?
Candollea														
cuneiformis	3	S.W. Australia	SX-M	shrub, 1-2 m.	L. S. 2-L. S. 3	M	±	572-1232	940	39	+	24	1402	m, t
huegelii	2	W. Australia	SX	shrub, 0.5 m.	L. S. 2	4.0 mm.	+	330-1265	573	13	+	8	738	m, th
uncinata	1	Interior of W. Australia	X	shrub, 0.2-0.5 m.	L. S. 1	3.0 mm.	+	330-853	547	13	+	4	767	m, th
Hemipleurandra														
lineata	1	W. Australia	SX	semi-prostrate shrub	L. S. 3 (?)	-		473-869	627	30	+	7	957	?
furfuracea	1	S.W. Australia	SX	shrub, 0.5-1.5 m.	L. S. 3	-		528-979	726	40	+	10	935	?
hypericoides	1	S.W. Australia	SX-M	shrub	L. S. 2	4.5 mm.	+	363-1056	616	20	+	7	792	m, t
Pleurandra														
sericea	2	E. Australia	SX	shrub, 0.5-1 m.	L. S. 2	3.3 mm.	+	363-1265	697	22	+	9	998	m, th
stricta	1	E. & S. Australia	SX	shrub, 0.5 m.	L. S. 1	3.2 mm.	+	193-770	481	17	+	8	759	m

TABLE 2. Summary of selected wood anatomical features of Hibbertia in relation to growth habit and habitat *(continued)*.

exutiacies	1	S.E. Australia	SX	prostrate shrub	L. S. 1	3.8 mm.	+	231-660	430	21	+	5	613	m
aspera	1	S.E. & W. Australia	SX	shrub	L. S. 2	3 mm.		352-792	561	?	+	7	770	?
Hemistemma														
coriacea	1	Madagascar	SX	shrub, 0.6-2 m.	L. S. 2-L. S. 3	M	-	693-1287	957	40	+	19	1474	m, t
banksii	1	N. Queensland, Australia; S. New Guinea	M	shrub, 1-2 m.	L. S. 3	-		671-1430	968	?	+	12	1144	?

[a]Symbols used: mesic (M), semi-xeric (SX), or xeric (X).

[b]Leaf size classes after Raunkiaer (1934): (L. S. 1) Leptophylls 0-25 mm.^{2}; (L. S. 2) Nanophylls 25-225 mm.^{2}; (L. S. 3) Microphylls 225-2025 mm.^{2}; (L. S. 4) Mesophylls 2,025-18,222 m^2.

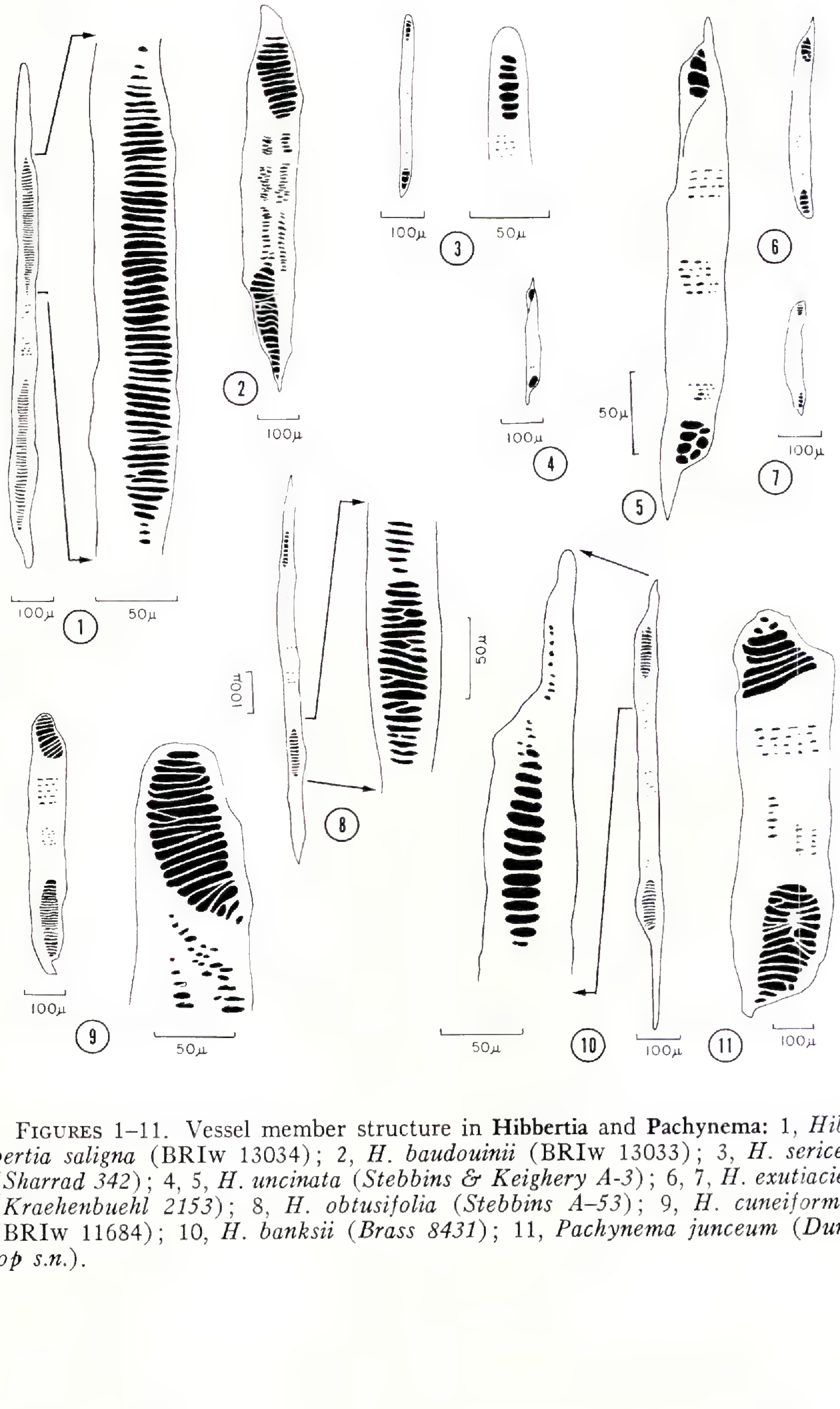
[c]Symbol used: mature wood (M).

[d]Symbols used: growth rings present (+), or absent (-).

[e]Symbols used: walls thin - lumen greater than thickness of walls (t); medium - lumen equal to thickness of walls (m); or thick - lumen less than thickness of walls (th).

[f]Symbol used: data unavailable (?).

Australia, is unusual in possessing extensive scalariform lateral wall pitting. Perforation plates are exclusively scalariform in the vast majority of species, although there is wide variation in the number of bars per perforation. In our material mean bar number ranges between a high of 42 and a low of 2 (FIGURES 1–10). Bars also vary considerably in width and degree of separation. Branched bars are frequent. It is of much interest



FIGURES 1–11. Vessel member structure in **Hibbertia** and **Pachynema:** 1, *Hibbertia saligna* (BRIw 13034); 2, *H. baudouinii* (BRIw 13033); 3, *H. sericea* (*Sharrad 342*); 4, 5, *H. uncinata* (*Stebbins & Keighery A-3*); 6, 7, *H. exutiacies* (*Kraehenbuehl 2153*); 8, *H. obtusifolia* (*Stebbins A–53*); 9, *H. cuneiformis* (BRIw 11684); 10, *H. banksii* (*Brass 8431*); 11, *Pachynema junceum* (*Dunlop s.n.*).

that simple perforation plates were observed in a low percentage of the vessel elements in *H. drummondii*, *H. glaberrima*, and *H. uncinata* (FIGURE 4). In these species vessel elements are occasionally present with simple perforations on one end and few-barred scalariform perforation plates on the other.

IMPERFORATE TRACHEARY ELEMENTS. Imperforate tracheary elements are fiber-tracheids, although in many of the small, semi-xeric species the pit borders are very reduced, and the elements approach the libriform fiber type. The mean length of the fiber tracheids generally ranges within the very short and short categories; only *Hibbertia lucens* and *H. ngoyensis* have imperforate tracheary elements that can be classified as long. Bordered pits are usually present on both radial and tangential walls and have minute to large diameters. In the New Caledonian species the pitting is often distributed in multiseriate rows. The walls of fiber tracheids vary considerably in thickness. Thin-walled elements (cell lumen greater than thickness of walls) occur in *H. scandens*, *H. baudouinii*, *H. lucens*, *H. trachyphylla*, *H. saligna*, *H. virgata*, *H. cuneiformis*, *H. hypericoides*, *H. coriacea*, and particularly *H. ngoyensis*. Thick-walled elements (cell lumen almost completely closed) characterize *H. glaberrima*, *H. huegelii*, *H. uncinata*, *H. sericea*, and particularly *H. drummondii*.

RAYS. Rays are heterogeneous, and in plants with abundant xylem both multiseriate and uniseriate rays are present. In Australian plants with limited secondary xylem production, generally only uniseriate rays occur, although these may occasionally become biseriate. Multiseriate rays are present in New Caledonian species in the first-formed secondary xylem. Multiseriate rays are 1 to 5, mostly 1 to 3, cells wide, are composed primarily of upright cells, and have long uniseriate wing extensions of the upright cells. Rays tend to be numerous to abundant per square mm.

AXIAL PARENCHYMA. Axial parenchyma is diffuse and scanty in distribution, although it becomes increasingly scarce in more xeric species. Axial parenchyma is rare in plants like *Hibbertia drummondii*. Numerous raphides are present in enlarged axial parenchyma cells of *H. cuneiformis* and *H. virgata*.

DISCUSSION

In the genus *Hibbertia*, trends of specialization with respect to growth habit have been chiefly toward small, thin-stemmed, prostrate or semi-prostrate shrubs; and with respect to leaves primarily toward leptophylls and nanophylls (*sensu* Raunkiaer, 1934) having various kinds of specializations associated with drought resistance. Nodal anatomy has frequently been reduced from the trilacunar to the unilacunar pattern. The resulting diversity in plant habit, and, therefore, the amount of secondary xylem produced, makes an evaluation of the wood anatomical data obtained from this genus difficult. The dangers in comparing data from woods of different

ages and growth habits are well known. Nevertheless, it is clear that *Hibbertia* has undergone an extensive adaptive radiation that has often resulted in reduced plant size in response to increasingly arid conditions. The combination of decreased plant stature and decreased water availability has produced significant alterations in xylem structure.

Hibbertia species from mesic habitats show an absence of growth rings. Seasonality of climate is reflected in xylem with growth rings and even ring porosity. In *Hibbertia*, vessel elements have frequently become shorter, a trend noted for other xeric taxa by Carlquist (1975), and their perforation plates have acquired a reduced number of bars (less than 10) with a few species even possessing occasional simple perforation plates. Small differences in vessel member length are not here regarded as important, although variation representing different size classes of elements is significant. In dicotyledons as a whole, these trends have usually been accompanied by an increase rather than a decrease in pore diameter. In *Hibbertia* a reduction in vessel element length is associated with a reduction in pore width. These tendencies are also combined with an increase in pore number per unit area. It must be kept in mind, however, that there has also occurred a dramatic decrease in the total amount of xylem produced in the xeric plants. The only exception in the trend toward smaller pore diameters in small-stemmed species is *H. scandens*, a liana, in which vessels are very wide in comparison with stem diameter, yet have retained scalariform perforation plates with a moderate bar number.

With regard to correlations between perforation plate type and ecological factors, van der Graaff and Baas (1974) and Carlquist (1975) presented evidence to show that no general trend can be established in dicotyledons as a whole, an opinion further enunciated and documented by Baas (1976). Individual genera, however, occasionally do show such correlations. *Hibbertia*, for example, demonstrates a high degree of correlation between mesic habitats and longer vessel elements with many-barred scalariform perforation plates, and xeric habitats and vessel elements with reduced length, diameter, and bar number in scalariform perforations. The only notable exception is the xeric species *H. procumbens*, which has short, narrow vessel elements, yet has retained scalariform perforation plates with a high number of bars. The scalariform lateral wall pitting on the vessel elements of this species is also unusual. It is very clear that in *Hibbertia*, habit-related anatomical modification is superimposed upon evolutionary, habit-related, and/or physiological specialization, and the separation of these facets is difficult.

Four other families of angiospermous shrubs occur regularly in association with the specialized Australian species of *Hibbertia*: Proteaceae, Leguminosae (especially *Acacia*), Myrtaceae, and Epacridaceae. In the first three families, vessel elements are short, comparatively wide, and have simple perforations. The Epacridaceae, however, resemble *Hibbertia* in that several species have vessel elements with small or very small diameters and scalariform perforation plates. The Proteaceae, Leguminosae, and Myrtaceae contain large shrubs and trees, and most of the recorded data

are from these larger species. The Epacridaceae, on the other hand, contain chiefly small, slender-stemmed shrubs similar in growth habit to *Hibbertia*. Baas (1976) has observed that in the Epacridaceae, the genera with scalariform plates show a mesic preference, and the genera with exclusively or predominantly simple plates prefer xeric habitats.

RELATION BETWEEN WOOD ANATOMY AND TAXONOMY. As reported by Stebbins and Hoogland (1976), the genus *Hibbertia* is remarkable for its great range of variation with respect to leaf size, shape, and structure, as well as to floral morphology. The present study reveals an additional large range of variation with respect to secondary xylem structure, particularly in vessel element morphology. In many of the principal sectional groups (*sensu* Gilg & Werdermann, 1925), which differ from each other with respect to floral morphology, the trend toward medium-sized to small, often acicular leaves can be found as an independent course of evolution (Rury & Dickison, 1977).

Within each section or sectional group (considering HEMIPLEURANDRA, HEMISTEMMA, and PLEURANDRA as a single group) there appear to be parallel trends of specialization. In leaf morphology they consist of reduction in leaf size and venation, and increase in the proportion of sclerenchymatous tissue; in floral morphology there has been reduction in size and number of parts; and in vessel elements, reduction in length, diameter, and number of scalariform perforation plate bars, all correlated with an overall reduction in plant size. A different combination is seen in *Hibbertia scandens* (section CYCLANDRA, subsection SUBSESSILES), in which larger leaves and flowers are associated with vessel elements showing no reduction in diameter. This species has also become specialized differently in growth habit, since it is a vine rather than a small shrub. The three New Caledonian sections exhibit considerable homogeneity in their wood anatomy. In addition, they have many similarities to section HEMISTEMMA, a relatively mesophytic species group from northern Australia, New Guinea, and Madagascar. A very interesting parallelism in leaf and nodal structure also occurs within these sections separated by floral characters. The New Caledonian subsection TRIMORPHANDRA, placed by Gilg and Werdermann (1925) within the highly heterogeneous Australian section CYCLANDRA on the basis of floral morphology, exhibits a leaf morphology identical to that of the New Caledonian hibbertias (Rury & Dickison, 1977). Although wood specimens of subsection TRIMORPHANDRA were not available for study, we strongly suspect that the wood anatomy of these species would serve to support the suggested transferral of this subsection to one of the New Caledonian sections of *Hibbertia*.

A lack of correlation is evident when *Hibbertia* is compared with two of its nearest relatives, *Didesmandra* and *Schumacheria*. These genera have longer vessel elements with larger numbers of scalariform perforation plate bars than any species of *Hibbertia* (Dickison, 1967). Nevertheless, their flowers are bilaterally symmetrical, and in the reduction of the ovules to one per carpel, as well as in floral anatomy, they are more special-

ized than any species of *Hibbertia* (Dickison, 1968; Wilson, 1973). *Pachynema*, the third genus related to *Hibbertia*, is essentially leafless and has a much reduced floral structure (Wilson, 1973). Examination of the secondary xylem of *P. junceum* (*van Steenis 17664* and *C. Dunlop s.n.*) reveals that vessel elements are medium sized in length (242–627 μm., mean 440 μm.) with scalariform perforation plates. The number of bars per scalariform perforation plate ranges from 2 to 15 with an average number of 7 (FIGURE 11). Fiber-tracheids are very short in length (363–902 μm., mean 660 μm.).

RELATION BETWEEN VESSEL ELEMENT STRUCTURE AND GEOGRAPHIC DISTRIBUTION. The species having the least specialized vessel elements include endemics to each of the major geographic regions where *Hibbertia* occurs (eastern Australia, southwestern Australia, New Caledonia, Madagascar) with the exception of northern Australia, from which no specimens have yet been examined. However, since the species of northern Australia resemble *H. coriacea* of Madagascar and *H. lucens* of New Caledonia in most characteristics, and occur in similar habitats, there is good reason to believe that most of them have relatively unspecialized vessel members. With the exception of *H. scandens*, which occurs from southeastern Australia northward to New Guinea, all of the species known to have more specialized vessel elements occur in southeastern, southwestern, or interior Australia, and inhabit temperate or subtropical rather than tropical regions. Trends toward leptophylly with accompanying reduction in length and diameter of vessel elements occur in species endemic to southeastern Australia (*H. virgata*), to the dry interior (*H. glaberrima*), and to southwestern Australia (*H. huegelii*), as well as in species groups that are distributed all across the continent (*H. stricta*). The three species observed to possess occasional simple perforation plates are all from the interior region of Australia. The evidence from geography, therefore, supports that from floral morphology to indicate that in various parts of temperate Australia, independent trends toward xylem specialization have occurred contemporaneously. Although in *Hibbertia* reduction in vessel member length and diameter is apparently the result of a multitude of biotic and abiotic factors, these trends do follow the general trends for other dicotyledons of decreased vessel element length and diameter with increasing latitude (van der Graaff & Baas, 1974).

RELATION BETWEEN WOOD STRUCTURE AND HABITAT. The trends of specialization of vessel elements toward shortening, reduction in diameter, reduction in the number of bars on scalariform perforation plates, and even the formation of simple plates, that are reported for the genus *Hibbertia* are clearly associated with occupation of drier habitats, including those like the heathlands of eastern Australia. Similar trends are reviewed by Carlquist (1975) for desert shrubs and high montane or alpine cushion plants belonging to various families. Associated with these changes in *Hibbertia* vessel structure, is a concomitant decrease in length and in-

crease in wall thickness of imperforate tracheary elements and an overall decrease in the amount of axial parenchyma. The species with the thickest fiber-tracheid walls is *H. drummondii*, a species also characterized by the occasional occurrence of simple perforation plates, which grows in the dry Australian interior.

Nevertheless, a different picture emerges when one compares the least specialized species belonging to each of the sections with each other, and also when *Hibbertia* is compared with other genera of Dilleniaceae. These species, although by no means xerophytic, do not always occupy the wetter habitats of the regions where they are found. *Hibbertia saligna*, a species with comparatively primitive vessel members, is generally distributed on ridge crests and mountainsides in a forest of *Eucalyptus* spp. This species of *Hibbertia*, because of the tendency of *Eucalyptus* leaves to hang vertically, receives abundant light on the forest floor. *Hibbertia serrata*, *H. cuneiformis*, and *H. lucens* are three additional species which possess vessel elements having scalariform perforation plates with 24 to 42 bars. The first two of these species grow in southwestern Australia where annual precipitation is ample, from 40 to 60 inches, but where the summer drought lasts from four to five months. In this region, they occur in relatively dry as well as more mesic sites. *Hibbertia lucens* has a tropical habitat, but according to herbarium labels it grows in dry, open forests rather than in wet rain forests. All of the New Caledonian species that were investigated have comparatively primitive vessel members. *Hibbertia baudouinii* occurs in more mesic situations than does *H. lucens*, and the specimen of *H. ngoyensis* studied grew in a humid forest. The remaining species having vessel elements with 20 or more bars per scalariform perforation plate are *H. coriacea* of Madagascar, which grows in the climatically moist eastern side of the island (but according to herbarium labels in dry, sunny places or on sandy soil that is subject to periodic drought), and *H. obtusifolia*, the specimen of which was collected in a dry *Eucalyptus* forest near Canberra, Australia. Fiber-tracheid walls of these plants tend to be thinner than in other species. Also, all of the above species of Madagascar and New Caledonia have a more regular, better-developed system of both low and high order venation.

Present evidence suggests, therefore, that the correlation between vessel element specialization and adaptation to drought holds well for trends within the Australian species of *Hibbertia*, but that the situation within the genus as a whole, particularly among the species of northern Australia, New Caledonia, and Madagascar, is less clear. Any conclusions about these species must await the study of additional material.

The same ambiguity arises when other genera of Dilleniaceae are examined. Long vessel members having exclusively scalariform perforation plates with many bars occur in *Dillenia*, *Schumacheria*, and *Didesmandra*. Whereas the latter two genera are rain forest plants, *Dillenia* grows in a variety of habitats including lowland rainforests, savannas, and monsoon forests with pronounced dry periods (Baas, 1976). Another dilleniaceous genus with scalariform perforation plates is *Acrotrema*, a woody herb that

grows in wet areas. These genera, however, are distinctly more specialized with respect to floral morphology than is *Hibbertia* (Dickison, 1968; Wilson, 1973), so they cannot be regarded as being more (or even as) closely related to the common ancestor of the Dilleniaceae than is *Hibbertia*. The presence in *Pachynema complanatum* of elongate vessel elements of which the scalariform perforation plates have 16 to 48 bars (Dickison, 1967) is truly remarkable, and a re-examination of this species with new material would be highly desirable. This species grows in the tropical monsoon climate of northern Australia where it is subjected to five months of winter drought. It is a shrublet bearing leafless, flattened stems and much-reduced flowers. The habit of the plant, and even more that of other species of *Pachynema*, such as *P. junceum*, suggests a long history of adaptation to aridity. The occurrence of scalariform elements in *Pachynema* suggests the possibility of an early derivation of this genus from the ancestral hibbertias and a subsequent radiation into xeric habitats, rather than a more recent derivation from the extreme xeromorphic forms of *Hibbertia*. Consequently, the anatomy and the ecological preferences of the least specialized species of Dilleniaceae do not support the hypothesis that their ancestor evolved in a tropical rain forest climate, and that specialization has been continuously and irreversibly associated with adaptation to greater aridity.

WOOD ANATOMY AND LEAF MORPHOLOGY IN RELATION TO HABITAT. Vegetative character syndromes observed in the growth habit, nodes, and leaves of numerous species of *Hibbertia* represent the evolutionary products of morphological adaptation within diverse ecological situations (Rury & Dickison, 1977). The present study reveals ecologically adaptive character syndromes in the wood anatomy of *Hibbertia* which are clearly correlated with both habit and habitat of the species studied (TABLE 3). It appears that the vegetative and wood anatomical character syndromes of these hibbertias have evolved, in general, as a single vegetative unit in response to environmental selection (TABLES 3, 4). Hence the wood anatomy, nodal structure, and leaf morphology and venation are best regarded as a "morphological continuum" which has evolved as a unit during the ancient adaptive radiation of this genus (*sensu* Stebbins, 1974).

The Australian hibbertias exhibit a heterogeneous species assemblage with respect to leaf size, leaf morphology, and floral structure. The most mesic species of Australia occur as small (*Hibbertia saligna*) to large (*H. serrata*) shrubs, or rarely vines (*H. scandens*, *H. dentata*). In these plants, features such as long, wide, scalariform vessel elements with numerous bars, and thin-walled fibers are correlated with mesomorphic leaves with primitive (*sensu* Hickey & Wolfe, 1975) leaf venation patterns. All mesophytic species examined, with the exception of *H. hypericoides*, possess three-trace, trilacunar nodes, a feature considered as primitive for *Hibbertia* and the entire family Dilleniaceae (Dickison, 1969). The presence of such features as short vessels with few bars (mean 7) per perforation plate, unilacunar nodes, reduced leaves (nanophylls), and reduced leaf venation in *H. hy-*

TABLE 3. Wood anatomical features and leaf sizes of 27 species of Hibbertia in relation to habitat type and geography.

SPECIES GROUPING	LEAF SIZE CLASS [a]	VESSEL ELEMENT LENGTH, μm.	PORE DIAMETER, μm.	NO. BARS PER PLATE	FIBER LENGTH, μm.	FIBER WALL THICKNESS [c]
Australian mesic						
(8 spp.) mean	L. S. 3	851	30	21	1059	m–t
range	L. S. 2, 3	308–1694	14–45	6–80	792–1402	
New Caledonian mesic						
(2 spp.) mean	L. S. 3	1023	76	20	1623	m–t
range	L. S. 3, 4	968–1078	57–95	17–22	1441–1804	
Total mesic species						
(10 spp.) mean	L. S. 3	885	42	21	1172	m–t
range	L. S. 2–4	308–1694	14–95	6–80	792–1804	
Australian semi-xeric						
(11 spp.) mean	L. S. 2	585	22	10	801	m
range	L. S. 1–3	165–1265	14–40	0–37	517–1402	t–th
Island semi-xeric [b]						
(4 spp.) mean	L. S. 3	863	45	29	1188	m–t
range	L. S. 2, 3	341–2037	35–61	13–50	1001–1551	
Total semi-xeric species						
(15 spp.) mean	L. S. 2	655	28	15	898	m
range	L. S. 1–3	165–2037	13–61	0–50	517–1551	t–th
Xeric species (Australian)						
(2 spp.) mean	L. S. 2	522	18	3.5	764	m–th
range	L. S. 1–3	497–547	13–23	3–4	760–767	

[a] Leaf size classes: see TABLE 2.
[b] Fiji, New Caledonia, and Madagascar.
[c] Fiber wall thicknesses: t, thin; m, medium; th, thick.

TABLE 4. **Wood anatomical features of 27 species of Hibbertia in relation to their leaf size classes.**

LEAF SIZE CLASSES [a]	VESSEL ELEMENT LENGTH, μm.	PORE DIAMETER, μm.	NO. BARS PER PLATE	FIBER LENGTH, μm.	FIBER WALL THICKNESS [c]
L. S. 1, 2 (12 spp.) mean	559	19	11	757	m
L. S. 2, 3 [b] (4 spp.) mean	726	28	12	1017	m
L. S. 3, 4 (11 spp.) mean	897	45	23	1206	m–t

[a] Leaf size classes: see TABLE 2.
[b] Excluding species with exclusively L. S. 2 or L. S. 3 leaves, i.e., leaves of intermediate sizes.
[c] Fiber wall thicknesses: t, thin; m, medium; th, thick.

pericoides, a species of semi-xeric and mesic habitats, suggests that this species may be a secondary radiant into mesic areas.

All of the mesophytic island species of *Hibbertia* exhibit a vegetative morphological strategy which differs from that of the mesophytic Australian hibbertias. The large shrubs and rosette trees of these island habitats possess trilacunar nodes and large, entire leaves with strong intramarginal veins and a very rigid, regular, and well-developed system of low (brochidodromous) and high order venation. These mesophytes, however, possess long, scalariform vessel elements which, with the exception of a slightly larger pore diameter, are very similar to those of their shrubby Australian counterparts. The non-expansible, tear-resistant leaves of these island hibbertias thus appear to represent the result of evolution within a relatively non-seasonal, growth-promoting habitat where the potential for sudden leaf expansion in response to ephemerally favorable microclimatic conditions would not be advantageous. The occurrence of such mesomorphically advanced leaf venation patterns in plants with relatively primitive wood anatomy represents a type of mosaic evolution which is also evident in other genera of Dilleniaceae.

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AN ETHNOFLORA OF CHOKOLOSKEE ISLAND, COLLIER COUNTY, FLORIDA

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CHOKOLOSKEE ISLAND, one of the largest of Florida's Ten Thousand Island group in Collier County, has a long history of habitation by man. Because of this extended occupation, its flora has shifted in species composition with each change of people. The native flora was mostly tropical hardwood hammock and mangroves; settlement by the Calusa Indians, the Spanish, the Seminoles, the English, and various groups from the United States has greatly altered the original plant associations. At present the island is experiencing what may prove to be the most traumatic shift. The newest change, increasing development, threatens to eliminate all traces of past eras. This study records what remains of the past, as well as present changes.

HISTORY

Primeval Chokoloskee differed from other islands in the area in being higher and protected in an isolated end of the back bay, now known as the Chokoloskee Bay. Here at the mouth of the Turner River, people from the north first settled about 2200 B.C. (Sears, 1956). The earliest recorded name for the descendants of these people, the Calusa, comes from the Spanish.

The proto-Calusa economy was fishing, hunting, and gathering, and was based on the locally abundant oyster (Cushing, 1896; Willey, 1949; Sears, 1956). Quahog clam, horse conch, and the lightning whelk were other important marine products. These were valued not only for their flesh, but also for their shells which were used for tools since suitable rocks were absent except as occasional trade items from the north. Terrestrial food in the form of deer, opossum, raccoon, and rabbits was also available. Perhaps the most important were birds, particularly turkeys and white ibis, and plant products. These filled the need for a good source of thiamin to counteract the problem of thiaminase. Thiamin (vitamin B_1) becomes a critical limiting factor in a diet consisting largely of raw shellfish since uncooked fish or shellfish is very high in this particular enzyme (Greig & Gnaedinger, 1971; Bethke *et al.*, 1973). The archeological record (Hrdlicka, 1922) and historical accounts (Barrientos, 1965; Solis de Meras, 1964) demonstrate that these Indians had no gross dietary inadequacies.

To supplement their animal diet, there was an ample vegetable larder. As a starch staple, the Calusa had both red coontie (*Smilax* spp.) and white coontie (*Zamia* sp.). Some zamia was gathered on the west coast, but the bulk was tribute from the subservient tribes of the east coast, where the plant was much more plentiful (Fontaneda, 1944).

The Calusa, and probably their predecessors, subjugated the Indians of the eastern Florida coast and extracted tribute from them (Swanton, 1922). Calusas thwarted all Spanish attempts to Christianize them and to enslave them for work in the gold mines of Hispaniola. This was in contrast to the Lucayans of the Bahamas, and a great proportion of the Matacumbe, Tequesta, and Jaega of southern Florida. Juan Ponce de León, a veteran of genocidal campaigns on both Puerto Rico and Santo Domingo, was repulsed and later died as a testament to Calusa ferocity.

European diseases and slaving drastically reduced the total aboriginal population of Florida. Spanish slave-hunting from the south declined by the early 1600's. In the mid-1600's English and Creek slave raids started, but this time the primary pressure was on the tribes of northern and central Florida. These factors caused the Calusa to shrink from a once-powerful tribe to a small group sequestered in the recesses of the lower western coast. From the early seventeenth century on, there is little or no record regarding the Calusa as a people or a culture.

The next group to inhabit this region, and without a doubt Chokoloskee itself, was a mixture of Cuban fishermen and Indians. The Indians were the so-called "Spanish Indians" who have been the subject of much investigation (Dodd, 1947; Goggin, 1950; Sturtevant, 1953; Neill, 1955). The most probable explanation of the Spanish Indians is that they were Calusa remnants; other accounts attempt to involve vanguard Seminoles and even Choctaws. The Indian-Cuban relationship was a peaceful, commercial arrangement advantageous to both.

There were numerous fishing "ranchos" located along the west coast from Tampa Bay southward, with a peak population of around 400 (Hammond, 1973). The first English language report concerning the "ranchos" was from Roberts (1976). Bernard Romans, surveyor for the British Crown, observed a commerce in 1769 of over 100 tons per year in dried and salted fish and corncob-smoked fish roe with the Havana market (Romans, 1962). Turtles, shark liver oil, songbirds, and "manufactured goods" were also important export items. Cardinals, which brought six to ten dollars each, were caught with a bird lime made from gum elemi, an extract of the gumbo limbo tree (*Bursera simaruba*) (Williams, 1962; Covington, 1959). Transported live to Havana in willow cages, these birds were especially favored among cigar makers, seamen, and the wealthier classes. Manufactured goods probably included surplus cordage termed "cuba." This cord was made by women from one of the various native or introduced plants, e.g., *Yucca aloifolia*, *Agave decipiens*, *Sansevieria metallica*, *Gossypium hirsutum*, *Hibiscus tiliaceus*.

Since this system of fishing "ranchos" was thriving at the beginning of the English administration of Florida (1763–1783), it had been an ongoing concern for quite some time, probably active to some degree by the late 1600's. The largest of these "ranchos" comprised eighteen or twenty palm-thatched huts with a population of fifty to sixty people including women and children (Williams, 1962). About half of the male population was Indian. The Cuban men often took Indian wives, but there was at

least one case in which a Spanish woman became the wife of a Spanish Indian warrior (Sprague, 1964). This Indian later participated in the raid on Indian Key in which Dr. Henry Perrine was killed in 1840. Perrine was at one time Consul to Yucatan and was particularly interested in the introduction of tropical crop plants into the United States (Robinson, 1942).

In typical Spanish tradition (cf. Kimber, 1973), these "ranchos" had small kitchen gardens in which corn, melons, several types of beans, limes, coconuts, and various kinds of aromatic herbs were grown. However, these dooryard gardens did not supply the bulk of their vegetables. The majority came from dealings with the many "plantations" in the area (Williams, 1962). In addition, coontie was obtained farther inland from less acculturated Indians.

These plantations were rarely over seven to eight acres and were located on the higher keys and on old kitchen middens and mounds along the rivers. Middens have since been favorite agricultural sites owing to the rich, black humus left when the tropical hardwood hammock is cleared. Elevation of the middens above sea level (8 to 20 feet) and their ease of access were added advantages. Corn, peas, melons, pumpkins, several kinds of beans, sweet potatoes, peppers, tomatoes, sugar cane, limes, oranges, and aromatic herbs were grown and sold at a high price to the relatively affluent fishermen. Most of the farmers were Cubans who seasonally employed several Indian families, but at least one Anglo-Saxon was recorded. John Durant, of Savannah, Georgia, farmed on Cape Romano in 1828, as did a mulatto whose name was not recorded (Williams, 1962).

Mullet fishing was such a lucrative enterprise that it induced Captain William Bunce, the customs inspector of Key West, to establish several "ranchos" of his own in Tampa Bay in 1834 (Dodd, 1947). After the onset of the Second Seminole War (1835–1842), Washington officials, particularly Joel Poinsett, Secretary of War, were highly suspicious of the "ranchos" and their Spanish Indians, believing that they were supplying the beleaguered Seminoles. Bunce, along with other prominent citizens, asserted that the Spanish Indians rarely visited the mainland, and spoke Spanish, and that the Seminoles never recognized them as fellow tribesmen. Notwithstanding, the "ranchos" were systematically closed down, and the Spanish Indians were shipped to Oklahoma (Foreman, 1953; Covington, 1954). Bunce's "ranchos" were burned by the U.S. Army as a suspected ". . . hiding place for a party of renegade Spaniards, who had previously and at this time [sic] intercourse with the savage band . . ." (Phelps, 1847).

In 1841 Lt. John T. McLaughlin, U.S.N., submitted to the Secretary of the Navy a map of southern Florida on which "Choko Lithka" appeared for the first time (Buker, 1975). The field reconnaissance for this map was made during the riverine campaign which decimated the Seminoles through every part of their former refugium, the Everglades. We do not know the particulars of the role of Chokoloskee during the Second Seminole War.

From 1842 to about 1870, few people frequented the Chokoloskee area.

Visitors were the occasional plume and hide hunters, the U.S. Army, and the Seminoles. There were also one or two Yankee families that intermittently farmed on the present site of Everglades City on the Barron River (then known as Potato Creek) in the 1860's (Tebeau, 1955). In 1856 an Army scout reported that on Chokoloskee, Seminoles had harvested about an acre of corn, and that about eight miles to the south of Pavionyhatchee (presently Chatham River), a twenty-acre crop of sweet potatoes had been dug. This field was located on an extensive mound system and was set about with clumps of sugar cane (Tebeau, 1968). This is the same agricultural site which was reconnoitered in 1838 by a similar expedition of the Second Seminole War (Covington, 1958). The last major expedition of the Third Seminole War (1855–1858) was launched into the Big Cypress Swamp from "Chokoliska Key." Chokoloskee appears on the famous 1856 "Ives Military Map" of South Florida. This reliable map has the distinction of being the first vegetation map of southern Florida that is not strictly the product of an active imagination. The name Chokoloskee is from the Muskogean Seminole, "chuko" — house, and "leske" — old. The reason for this name is unknown (Simpson, 1956), but one may speculate that it made reference to an ancient place of habitation.

With the advent of modern settlement of Chokoloskee in the early 1870's, signs of previous occupation were found in the form of several large lime trees (Tebeau, 1957). Latins from Key West formed about half of the population in these early years, with an array of "Anglos" from diverse parts constituting the other half.

The prevalent house type of this period was the "trash house," which had not only a palm thatch roof, but thatch walls as well. Some of these were quite elaborate, having a frame door with hinges. Usually a person had one in which to live and several that served as sheds. Trash houses were notorious fire hazards, so each family would have several sets sequentially (cf. Simpson, 1920). There are no wild palms to be found on the island today, nor were there any when the Smallwood family moved there in 1897. The primary thatching palms were the cabbage palm (*Sabal palmetto*), the saw palmetto (*Serenoa repens*), and the Florida thatch palm (*Thrinax radiata*). There was also heavy pressure on the thrinax for its trunks for use as poles to construct turtle crawls for which they are highly suited (Small, 1925, 1929).

Farming, fishing, hunting, and charcoal-making were the available livelihoods on Chokoloskee. Farming was primarily for the large population (20,000 in 1910) of Key West. Cigar-making was a flourishing industry near the turn of the century, and the southernmost city proved to be a reliable truck market (Cutler, 1923). Winter produce not sold in Key West was shipped via Mallory Line Steamers to New York. Both temperate and tropical crops were produced in great abundance. Tomatoes, cabbage, sugar cane, avocados, potatoes, peppers, cucumbers, eggplants, melons, onions, and bananas (the apple variety was preferred, although plantains or horse bananas tolerate more salt) were the main crops. Guavas, sugar apples, Jamaica apples, both sweet and sour oranges, cauliflowers, and

pumpkins were also sold. It seems strange that certain Cuban mainstays such as boniato, yuca, malanga, annatto, and beans were not produced, even though there were Cubans on Chokoloskee and Key West. Over three-fourths of the island was cleared and planted, with a preference for the high shell mounds for tomatoes, and the lower, heavier areas for sugar cane (Tebeau, 1955). In 1912 the Overseas Railroad was completed from the southeastern coast to Key West, and vegetables which could be produced more cheaply on the mainland were shipped in by rail. With the railroad came the end of Chokoloskee's farming era, although the large seedling avocado grove which spanned the island was still in heavy production until it was ruined by the 1926 hurricane. These "alligator pears" were packed in barrels and shipped north to Fort Myers and Punta Gorda, where as luxury items they brought a nickel each (Tebeau, 1955). All that presently remains of the grove is about 25 erratic seedling trees, from which all the fruit is either consumed or sold locally.

Making charcoal from buttonwood (*Conocarpus erectus*) and cutting these trees for sale were also important occupations of the early pioneers on the island. Buttonwood charcoal, even-burning and smokeless, was produced for the Key West market. It was made as follows: wood was cut into 3- to 4-foot lengths, neatly stacked into great semiconical piles reminiscent of wigwams, 6 to 9 feet high and 15 to 25 feet in diameter; each pile was then covered with sand and grass, leaving a vent in the top and several openings around the bottom to fire the wood and allow the gases to escape. If the wood cutters were not going to watch the fire all night after it was started, they would simply close up the vents. By this method, a cord of wood yielded ten bags of marketable charcoal. While activity ceased about 1930, as late as 1954 one could still see areas on the southwest Florida coast where the practice took place.

Occasional work was also found at the tanbark factory at Shark River, where the red mangrove (*Rhizophora mangle*) yielded an exceptionally high-quality tannic acid. This factory was intermittently operated from 1908 to 1923. The gathering of mature royal palms (*Roystonea elata*), used in development and landscape schemes in such places as Fort Myers and Tampa, also offered temporary work (Small, 1929).

Since the 1930's fishing has remained the chief occupation. Today commercial fishing for mullet and stone crabs is the mainstay of the economy, along with increasing tourism based on sport fishing and charter boats made famous by the Everglades Rod and Gun Club of Everglades City. A causeway was built from Everglades City to Chokoloskee in 1955; this helped the island's depauperate economy, but ended its insular mystique.

ETHNOFLORA

As is widely known, man is one of the most effective vectors for plant dispersal. The present project began as an attempt to determine whether the plants now growing on the island could be used to trace occupation by the various people who have lived on Chokoloskee. We soon discovered

that the post-Columbian plants could be recognized and assigned, in part, to a definite period. Those plants native to Florida, on the other hand, presented greater difficulty. Many of the plants included in this list were commonly used by prehistoric and historic inhabitants of Chokoloskee, yet their wide distribution does not necessarily implicate man as a vector. *Bursera simaruba*, for example, may be found in almost any hammock along the coasts south of Tampa; it is distributed by birds which eat the seeds. Conversely, *Sapindus saponaria* has been cited by Craighead (1974) as an indicator of Calusa habitation.

About 42 percent of the plants present, but not now cultivated, on Chokoloskee can be attributed directly to movement by man and to his activities. Many of these plants are exotics whose introduction into Florida can be traced to the 1800's and 1900's. Some plants have been brought in from the north (e.g., *Lepidium*, *Portulaca*), but the majority came from the West Indies and from Old World floras.

There is good documentation for many of the species listed having been used by man in Florida. For others there is no record here, but usage has been recorded elsewhere. In such cases we have usually assumed that similar utilization occurred on Chokoloskee. No attempt has been made to cite original sources for the use of plants or their products; instead, we have used recent, readily available publications for documenting most of them.

FLORISTIC COMPOSITION

In southern Florida the high ground usually associated with hammock vegetation has long been favored for habitation. Anthropologists do not believe that the mounds on the Turner River north of Chokoloskee were built by the Calusa solely for the advantage of elevation (Sears, 1956). They were partially the by-product of living and were part of a religious complex. One cannot help believing, however, that these elevated sites were refugia during storms. Particularly convincing evidence for this conclusion was given by Jonathan Dickinson, who weathered a hurricane in an Indian hut atop a shell mound on the Florida east coast in the 1600's (Dickinson, 1945). Accounts of early pioneer life of Chokoloskee (Tebeau, 1955) and other areas with hammocks (Tebeau, 1968; Pierce, 1970) indicate that the European and American settlers sought out hammocks for homesites. Similarly, the Seminoles used hammocks as temporary and permanent campsites (Tebeau, 1968).

A comparison of plant exploitation on Chokoloskee and in some other areas may be profitably made. Yarnell (1964) has reported that in the Great Lakes region about 20 percent of the vascular plants were used by Indians in pre-Columbian times. We know of no similar studies for other areas, but Griffin (1967) was of the opinion that this 20 percent usage might be taken as a standard of comparison.

The data for Florida hammocks must be interpreted with caution (Table 1). Of the hammocks listed, the Boynton Hammock apparently has

TABLE 1. **Ethnofloristic composition of certain Florida hammocks.***

HAMMOCK NAME	ETHNIC GROUPS	USAGE	ETHNOFLORA
Chokoloskee Island	Calusas, Spanish, Seminoles, Americans	Farming, settlement	83%
Lignum Vitae Key	Matacumbes, Spanish, Americans	Settlement, farming	60%
Butts hammock	Americans	Settlement, plant nursery	31%
Matheson hammock	Tequestas, Seminoles, Spanish, Americans	Settlement, public park	31%
Indian Key	Matacumbes, Spanish, Americans	Settlement	30%
Boynton hammock	Jaegas, Americans	Campsite	27%

* Note: these figures are based on the assumption that all species with a record of use were indeed used.

been least disturbed by man (Austin & Weise, 1972). Indian Key was occupied by Matacumbes and American pioneers, but has not been settled recently. Butts and Matheson hammocks (Avery, 1968; Austin, 1974) apparently have been subjected to little intrusion and disturbance. Only on Lignum Vitae Key (Avery, 1969; Popenoe & Avery, 1971) and on Chokoloskee are there records of both long and recent disturbance, and of the introduction of exotic plants. Thus the data seem to indicate that the ethnofloristic composition is not only a function of plant usage, but also of the recency of arrival and of the length of time used. Chokoloskee and Lignum Vitae have both the longest and the most recent histories of intrusion, and they correspondingly have the largest percentage of plants used.

The 20 percent figure for aboriginal utilization may be more realistic than total ethnofloristic composition appears to indicate. For Boynton hammock the 27 percent status indicates only slight European/American influence. Of the 29 assumedly utilized plants, 11 are documented to have been introduced from Old World sources. Thus, aboriginal use may have been only 17 or 18 percent of the present flora. For Chokoloskee, 29 species can be clearly documented as post-Columbian. These account for 21 percent of the plants not presently cultivated. Some of the remaining plants cannot be categorized with confidence, but the number used by the Calusa is probably near 20 percent.

For the ethnoflora of Chokoloskee, we have determined five categories of usage: 1) food and household plants, 50 species; 2) escaped or persistent ornamentals, 20 species; 3) medicinal and poisonous plants, 21 species; 4) homovectant weeds, 28 species; and 5) plants presently cultivated, 90 species. Those species used for more than one purpose have been counted twice. The remaining 40 species (about 17 percent of the flora)

consist of native plants having no apparent association with man. The ethnoflora in its broadest sense includes almost 83 percent of the island flora.

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APPENDIX. The Ethnoflora.

A. PLANTS NOT PRESENTLY IN CULTIVATION ON CHOKOLOSKEE ISLAND.

Abrus precatorius L. (Fabaceae). ROSARY PEA. Seeds poisonous (Hardin & Arena, 1974).

Acacia farnesiana (L.) Willd. (Fabaceae). WEST INDIAN BLACKTHORN. Cultivated for aromatic flowers and medicinal gum.

Acacia torulosa (L.) Willd. (Fabaceae). TWISTED ACACIA. Wood used outside of Florida.

Albizia lebbeck Bentham (Fabaceae). WOMAN'S TONGUE. Cultivated as an ornamental and for medicine (Morton & Ledin, 1952).

Alternanthera ramosissima (Martius) Moq. ex Chodat (Amaranthaceae). CHAFF-FLOWER. No known use by man.

Amaranthus viridis L. (Amaranthaceae). PIGWEED. Homovectant.

Annona squamosa L. (Annonaceae). SUGAR APPLE. Cultivated for food.

Ardisia escallonioides Schlecht. & Cham. (Myrsinaceae). MARLBERRY. Leaves used by the Mikasukis to season their tobacco (Morton, 1968).

Argemone mexicana L. (Papaveraceae). MEXICAN POPPY. Both herbage and seeds are poisonous (Muenscher, 1951), but the plants have been used as a narcotic.

Arundo donax L. (Poaceae). GIANT REED. Ornamental.

Atriplex arenaria Nutt. (Chenopodiaceae). BEACH-ORACH. No known use by man.

Avicennia germinans (L.) L. (Avicenniaceae). BLACK MANGROVE. According to Morton (1968), the seeds are edible when cooked.

Batis maritima L. (Bataceae). SALTWORT. Edible raw or cooked (Morton, 1968).

Bidens pilosa L. (Asteraceae). SPANISH NEEDLES. Leaves edible, juice medicinal (Morton, 1968); leaves used for tea.

Blechum brownei Juss. (Acanthaceae). Homovectant.

Borreria ocimoides (Burman f.) DC. (Rubiaceae). No known use by man.

Bryophyllum pinnatum Kurz (Crassulaceae). LIVE-FOREVER. Medicinal (Morton & Ledin, 1952).

Bumelia celastrina H.B.K. (Sapotaceae). SAFFRON PLUM. Fruits edible (Morton, 1968).

Bursera simaruba (L.) Sarg. (Burseraceae). GUMBO LIMBO. Sap used as bird lime; soft wood used for floats on nets and harpoons; leaves used as tea (Hedrick, 1919) and cattle food (Romans, 1962).

Caesalpinia bonduc (L.) R. Br. (Fabaceae). GRAY NICKER. Seeds used as malaria remedy (Morton & Ledin, 1952).

Capparis cynophallophora L. (Capparaceae). JAMAICA CAPER TREE. No known use by man.

Capparis flexuosa L. (Capparaceae). FLEXIBLE CAPER. No known use by man.

Capraria biflora L. (Scrophulariaceae). GOATWEED. Homovectant.

Capsicum frutescens L. (Solanaceae). BIRD PEPPER. Fruits preserved in vinegar and used as condiments (T. Smallwood, pers. comm.; D'Arcy & Eshbaugh, 1974).

Cardiospermum halicacabum L. (Sapindaceae). HEART SEED. Ornamentals (Long & Lakela, 1971); used as food in Ceylon.

Carica papaya L. (Caricaceae). PAPAYA, PAPAW. Leaves, stems, fruits, and roots eaten; leaves smoked as a remedy for asthma (Morton, 1968).

Cassia obtusifolia L. (Fabaceae). SICKLE POD, COFFEE WEED. Homovectant; seeds used as coffee substitute.

Cenchrus echinatus L. (Poaceae). SANDBUR. Homovectant.

Cenchrus incertus M. A. Curtis (Poaceae). Homovectant.

Chamaesyce blodgettii (Engelm. & Hitchc.) Small (Euphorbiaceae). SPURGE. Homovectant.

Chamaesyce hirta (L.) Millsp. (Euphorbiaceae). SPURGE. Homovectant.

Chamaesyce hypericifolia (L.) Small (Euphorbiaceae). SPURGE. Homovectant.

Chamaesyce hyssopifolia (L.) Small (Euphorbiaceae). SPURGE. Homovectant.

Chamaesyce porterana Small (Euphorbiaceae). SPURGE. Homovectant.

Chiococca alba (L.) A. Hitchc. (Rubiaceae). SNOWBERRY. No known use by man.

Chrysophyllum oliviforme L. (Sapotaceae). SATINLEAF. Fruits edible; wood used (Small, 1933); now an ornamental.

Citrus sinensis (L.) Osbeck (Rutaceae). SWEET ORANGE (temple variety). Cultivated for food.

Clerodendrum philippinum Schauer (Verbenaceae). CHRISTMAS ROSE, JAPANESE ROSE. Ornamental.

Coccoloba diversifolia Jacq. (Polygonaceae). PIGEON PLUM. Fruits eaten by Mikasukis (Morton, 1968).

Commelina diffusa Burman f. (Commelinaceae). DAYFLOWER. Homovectant.

Conocarpus erectus L. (Combretaceae). BUTTONWOOD. Wood used in making charcoal in the early 1900's.

Crotalaria incana L. (Fabaceae). RATTLEBOX. Homovectant.

Crotalaria pallida Aiton (Fabaceae). Homovectant.

Cynanchum sp. (Asclepiadaceae). Not seen in fruit or flower; no known use by man.

Cyperus ligularis L. (Cyperaceae). SAWGRASS. No known use by man.

Dactyloctenium aegyptium (L.) Richter (Poaceae). EGYPTIAN GRASS. Homovectant.

Desmodium tortuosum (Sw.) DC. (Fabaceae). TICK TREFOIL. Introduced as a forage crop; now naturalized.

Dicliptera assurgens (L.) Juss. (Acanthaceae). No known use by man.

Dioscorea bulbifera L. (Dioscoreaceae). POTATO VINE. Ornamental; used as food.

Distichlis spicata (L.) Greene (Poaceae). SALT GRASS. No known use by man.

Eragrostis ciliaris (L.) R. Br. (Poaceae). LOVE GRASS. Probably homovectant.

Erythrina herbacea L. (Fabaceae). CORAL BEAN. Seeds poisonous.

Eugenia axillaris (Sw.) Willd. (Myrtaceae). WHITE STOPPER. Fruits edible; wood used for cabinets (Small, 1933).

Eugenia foetida Pers. (Myrtaceae). SPANISH STOPPER. Perhaps used like *E. axillaris*.

Eupatorium odoratum L. (Asteraceae). No known use by man.

Ficus aurea Nutt. (Moraceae). STRANGLER FIG. Fruits eaten; latex used by Mikasukis to prepare a masticatory rubber (Neill, 1956).

Fimbristylis caroliniana (Lam.) Fernald (Cyperaceae). SEDGE. No known use by man.

Fimbristylis spathacea Roth (Cyperaceae). SEDGE. Homovectant.

Forestiera segregata (Jacq.) Krug & Urban (Oleaceae). FLORIDA PRIVET. No known use by man.

Galactia macreei M. A. Curtis (Fabaceae). MILK PEA. No known use by man.

Gouania lupuloides (L.) Urban (Rhamnaceae). CHEW STICK. Stems used as toothbrushes; reported to have medicinal properties (Hedrick, 1919).

Hamelia patens Jacq. (Rubiaceae). FIREBUSH. Ornamental.

Heliotropium angiospermum Murray (Boraginaceae). No known use by man.

Hylocereus undatus (Haw.) Britton & Rose (= *Cereus undatus* Haw.) (Cactaceae). NIGHT-BLOOMING CEREUS. Ornamental.

Hyptis pectinata (L.) Poiret (Lamiaceae). Homovectant.

Ipomoea alba L. (Convolvulaceae). MOONFLOWER. Most often cultivated for flowers, although leaves said to be edible (Morton, 1968).

Ipomoea carnea Jacq. (Convolvulaceae). BUSH MORNING GLORY. Ornamental.

Ipomoea hederifolia L. (Convolvulaceae). QUAMOCLIT. Cultivated and naturalized.

Ipomoea indica (Burman f.) Merrill (Convolvulaceae). MORNING GLORY. No known use in Florida. Cultivated elsewhere.

Ipomoea macrantha Roemer & Schultes (Convolvulaceae). BEACH MOONFLOWER. The young stems are used as pig food in Great Inagua, but no known use in Florida.

Ipomoea triloba L. (Convolvulaceae). Probably introduced from West Indies in ballast.

Iresine diffusa Humb. & Bonpl. ex Willd. (Amaranthaceae). BLOODLEAF. No known use by man.

Kalanchoë grandiflora A. Rich. (Crassulaceae). LIFE-PLANT. Ornamental. Naturalized.

Laguncularia racemosa (L.) Gaertner f. in Gaertner (Combretaceae). WHITE MANGROVE. Wood occasionally used.

Lantana involucrata L. (Verbenaceae). BEACH SAGE. No known use by man.

Lantana ovatifolia Britton (Verbenaceae). LANTANA. Fruits may be poisonous (Morton, 1968).

Lepidium virginicum L. (Brassicaceae). PEPPER-GRASS. Used by some as a condiment (Morton, 1968). Now a weed on Chokoloskee and perhaps homovectant.

Ligustrum ovalifolium Hassk. (= *L. amurense* Carr. ?) (Oleaceae). PRIVET. Persistent from cultivation as an ornamental.

Lycium carolinianum Walter (Solanaceae). CHRISTMAS BERRY. No known use by man. Eaten by birds, particularly the mockingbird.

Mastichodendron foetidissimum (Jacq.) Cronquist (Sapotaceae). MASTIC. While now absent from the island, there were three plants in the early 1900's (Thelma Smallwood, pers. comm., 1974). Fruits eaten; wood used (MacCauley, 1884).

Melanthera parviflora Small (Asteraceae). No known use by man.

Melia azedarach L. (Meliaceae). CHINABERRY. Persistent or occasionally naturalized. Ornamental; wood formerly used (Small, 1933).

Melothria pendula L. (Cucurbitaceae). CREEPING CUCUMBER. Fruits eaten (Morton, 1968) although strongly laxative (Hardin & Arena, 1974).

Mentzelia floridana Nutt. (Loasaceae). POOR-MAN'S-PATCH. No known use by man. Said to be the inspiration for "Velcro."

Morinda royoc L. (Rubiaceae). CHEESEWEED. No known use by man.

Momordica charantia L. (Cucurbitaceae). BALSAM APPLE. Medicinal and poisonous (Morton, 1968; Hardin & Arena, 1974), but used as food.

Opuntia stricta var. *dillenii* (Ker.) L. Benson (Cactaceae). PRICKLY PEAR. Fruits and perhaps pads eaten.

Oxalis corniculata L. (Oxalidaceae). LADY'S SORREL. Eaten by some people as greens. The plants are largely homovectant.

Panicum maximum Jacq. (Poaceae). GUINEA GRASS. Introduced as pasture plants by the 1780's (Parsons, 1972); now widely naturalized.

Parietaria floridana Nutt. (Urticaceae). PELLITORY. Probably homovectant.

Parthenocissus quinquefolia (L.) Planchon (Vitaceae). VIRGINIA CREEPER. No known use by man. Fruits said to be poisonous.

Pectis leptocephala (Cassini) Urban (Asteraceae). Used in a tea.

Persea americana Miller (Lauraceae). AVOCADO. During the early 1900's groves of these trees covered much of the southern end of the island (Tebeau, 1955). The 1910 hurricane damaged the crop, but fruit continued to be produced commercially. In 1926 a hurricane destroyed most of the trees, and market production ceased. There are still scattered trees on the island.

Petiveria alliacea L. (Phytolaccaceae). GUINEA-HEN WEED. Homovectant.

Philoxerus vermicularis (L.) Beauv. (Amaranthaceae). Morton (1968) said that the leaves may be eaten.

Phlebodium aureum (L.) Sm. (Polypodiaceae). CABBAGE PALM FERN. No known use by man.

Phoenix dactylifera L. (Arecaceae). DATE PALM. Fruits eaten. Plants persistent from cultivation.

Phragmites australis (Cav.) Trin. ex Steudel (Poaceae). REED. Often called *P. communis* Trin., but Adams (1972) and Gillis (1974), among others, have pointed out that this is a later name. Roots eaten raw, and sap used as sugar (Hedrick, 1919).

Piscidia piscipula (L.) Sarg. (Fabaceae). FISH POISON TREE. Bark used to poison fish.

Pisonia aculeata L. (Nyctaginaceae). PULL-AND-HOLD-BACK. No known use by man.

Pithecellobium unguis-cati (L.) Bentham (Fabaceae). CAT'S-CLAW. Arils eaten.

Plumbago scandens L. (Plumbaginaceae). WILD PLUMBAGO. No known use, except possibly ornamental.

Poinsettia cyathophora (Murray) Klotzsch & Garcke (Euphorbiaceae). WILD POINSETTIA. No known use by man.

Portulaca oleracea (L.) Sarg. (Portulacaceae). PURSLANE. The seeds used in a gruel by the Seminoles (Morton, 1968); the herbage eaten. Still cultivated in the Bahamas.

Psidium guajava L. (Myrtaceae). GUAVA. Introduced for edible fruits; naturalized.

Psychotria nervosa Sw. (Rubiaceae). WILD COFFEE. Seeds may have been used as a coffee substitute if the name is indicative.

Randia aculeata L. (Rubiaceae). INDIGO BERRY. Burkill (1966) lists the berries as a dye in the West Indies.

Rhabdadenia biflora (Jacq.) Muell.-Arg. (Apocynaceae). RUBBER VINE. No known use by man.

Rhizophora mangle L. (Rhizophoraceae). RED MANGROVE. Wood used for cabinets; bark used for dying and tanning.

Rhynchelytrum repens (Willd.) C. E. Hubbard (Poaceae). NATAL GRASS. Introduced as a pasture grass (Small, 1933); now widely naturalized.

Rhynchosia parvifolia DC. (Fabaceae). SNOUT BEAN. No known use by man.

Rivina humilis L. (Phytolaccaceae). BLOODBERRY. No known use by man.

Russelia equisetiformis Schlecht. & Cham. (Scrophulariaceae). CORAL PLANT. Ornamental and persistent.

Sansevieria metallica Gérome & Labroy (Liliaceae). BOWSTRING HEMP. Cultivated for cordage. Persistent and naturalized.

Sapindus saponaria L. (Sapindaceae). SOAP BERRY TREE. Leaves and fruits used as a soap substitute.

Scoparia dulcis L. (Scrophulariaceae). SWEET BROOM. Leaves used as a medicinal tea in the Philippines (Hedrick, 1919).

Sesbania exaltata (Raf.) Cory (Fabaceae). No known use by man.

Sida acuta Burman f. (Malvaceae). INDIAN MALLOW. Burkill (1966) stated that the plant has been used as a medicine and a fiber source in the Old World.

Solanum americanum Miller (Solanaceae). NIGHTSHADE. Green fruits poisonous; ripe fruits edible (Heiser, 1969).

Solidago stricta Aiton (Asteraceae). GOLDENROD. No known use in Florida.

Sonchus oleraceus L. (Asteraceae). Introduced and naturalized. Leaves and roots edible (Hedrick, 1919).

Sophora tomentosa L. (Fabaceae). NECKLACE POD. Said to have been used as a hallucinogen by Indians.

Spartina patens (Aiton) Muhl. (Poaceae). CORDGRASS. Although sometimes used as forage, these are a normal part of the coastal marsh vegetation.

Sporobolus domingensis (Trin.) Kunth (Poaceae). DROPSEED. Perhaps used as a forage.

Stachytarpheta jamaicensis (L.) Vahl (Verbenaceae). BLUE PORTERWEED. Used as a medicine in the Old World (Burkill, 1966) and to brew a porter in the West Indies.

Stylosanthes biflora (L.) B.S.P. (Fabaceae). PENCIL-FLOWER. No known use by man.

Suaeda linearis (Ell.) Moq. (Chenopodiaceae). SEA BLITE. Leaves edible.

Tecoma stans (L.) Kunth (Bignoniaceae). YELLOW ELDER. Medicinal, but perhaps only ornamental and naturalized on Chokoloskee.

Thespesia populnea (L.) Solander ex Correa (Malvaceae). SEASIDE MAHOE. Small (1910) recorded the first appearance of this tree on the mainland from a collection in Dade County in 1905, although it had been in the Keys for years. No known use by man.

Tillandsia balbisiana Schultes (Bromeliaceae). WILD PINE. Cultivated for ornament, and persistent.

Tillandsia fasciculata Sw. (Bromeliaceae). CARDINAL AIR PLANT. Only one plant has been found on the island. No known use.

Tillandsia flexuosa Sw. (Bromeliaceae). BANDED WILD PINE. Only one plant has been found. No known use.

Tillandsia setacea Sw. (Bromeliaceae). NEEDLE-LEAF WILD PINE. Persistent from cultivation at an old homesite.

Toxicodendron radicans (L.) Kuntze (Anacardiaceae). POISON IVY. Used as a medicine by some groups of people.

Trichostigma octandrum (L.) H. Walter (Phytolaccaceae). Small (1910) recorded this plant in Florida only on Chokoloskee. George N. Avery (pers. comm., 1972) has found it recently; we have not seen the plant.

Tridax procumbens L. (Asteraceae). Homovectant.

Verbesina virginica L. (Asteraceae). Frostweed. No known use by man.
Vigna luteola (Jacq.) Bentham (Fabaceae). Cow pea. No known use in Florida.
Waltheria indica L. (Sterculiaceae). Waltheria. Small (1933) said that the plants were "reputed to have medicinal properties." Homovectant.
Zanthoxylum fagara (L.) Sarg. (Rutaceae). Wild lime. No known use of this species, although others are known as "toothache tree" because of numbing properties.

B. Plants presently cultivated on Chokoloskee Island.

Acalypha wilkesiana Muell.-Arg. (Euphorbiaceae). Copperleaf. Ornamental.
Agave americana L. (Agavaceae). Century plant. Ornamental. Two varieties occur on the island: var. *marginata* Trel. and var. *variegata* Hort.
Allium cepa L. (Amaryllidaceae). Onion. Food.
Aloë barbadensis Miller (= *A. vera* L.) (Liliaceae). Barbados aloe. Ornamental and medicinal.
Anthurium sp. (Araceae). Ornamental.
Araucaria columnaris (Forster) Hooker (Araucariaceae). Norfolk Island pine. Ornamental. Possibly *A. heterophylla* (Salisb.) Franco also; not seen.
Arecastrum romanzoffianum Becc. (Arecaceae). Queen's palm. Ornamental.
Asparagus densiflorus (Kunth) Jessop (Liliaceae). Asparagus fern. Ornamental.
Asparagus setaceus (Kunth) Jessop (Liliaceae). Asparagus fern. Ornamental.
Bauhinia variegata L. (Fabaceae). Orchid tree. Ornamental.
Bombax malabaricum DC. (Bombacaceae). Red silk-cotton tree. Ornamental.
Bougainvillea glabra Choisy (Nyctaginaceae). Bougainvillea. Ornamental.
Brassaia actinophylla F. Mueller (Araliaceae). Umbrella tree. Ornamental.
Brassica oleracea L. (Brassicaceae). Cabbage. Food.
Callistemon lanceolatus Sw. (Myrtaceae). Bottle-brush. Ornamental.
Cananga odorata Hooker f. & Thomson (Annonaceae). Ylang-ylang. Ornamental; aromatic flowers.
Caryota mitis Lour. (Arecaceae). Fishtail palm. Ornamental.
Casuarina equisetifolia L. (Casuarinaceae). Australian pine. Ornamental; wind-break.
Casuarina glauca Sieb. (Casuarinaceae). Beefwood. Ornamental.
Catharanthus roseus (L.) Don (Apocynaceae). Periwinkle. Ornamental. Widely naturalized in Florida.
Cereus peruvianus Haw. (Cactaceae). Hedge cactus. Ornamental.
Chrysalidocarpus lutescens Wendl. (Arecaceae). Cane palm. Ornamental.
Citrus aurantifolia Swingle (Rutaceae). Lime, Key lime. As an ornamental and for food.
Citrus aurantium L. (Rutaceae). Sour orange. Ornamental.
Citrus paradisi Macf. (Rutaceae). Grapefruit. For food and as an ornamental.
Coccoloba uvifera L. (Polygonaceae). Sea grape. Ornamental.
Cocos nucifera L. (Arecaceae). Coconut. As an ornamental; rarely for food. Lethal yellowing, a mycoplasma-induced, lethal infection has not yet hit the island, although it is in Everglades City.
Codiaeum variegatum (L.) Blume (Euphorbiaceae). Croton. Ornamental.
Cordia sebestena L. (Boraginaceae). Geiger tree. Ornamental.
Cordyline australis (Forster) Hooker f. (Liliaceae). Dracena. Ornamental.
Coleus blumei Bentham (Lamiaceae). Coleus. Ornamental.
Crinum sanderianum Baker (Amaryllidaceae). Milk and wine lily. Ornamental.

Cryptostegia madagascariensis Bojer (Asclepiadaceae). PURPLE ALAMANDA. Ornamental.
Cucurbita moschata Duchesne (Cucurbitaceae). SQUASH. Food.
Cyperus alternifolius L. (Cyperaceae). UMBRELLA PLANT. Ornamental.
Delonix regia (Bojer) Raf. (Fabaceae). POINCIANA. Ornamental.
Dizygotheca elegantissima Vig. & Guill. in Lecomte (Araliaceae). FALSE ARALIA. Ornamental.
Epiphyllum sp. (Cactaceae). NIGHT-BLOOMING CACTUS. Ornamental.
Eriobotrya japonica (Thunb.) Lindl. (Rosaceae). LOQUAT. As an ornamental, and for shade and edible fruits.
Eucalyptus grandis Hill ex Maiden (Myrtaceae). BROWN GUM. Ornamental.
Eugenia uniflora L. (Myrtaceae). SURINAM CHERRY. Ornamental.
Euphorbia lactea Haw. (Euphorbiaceae). CANDELABRA CACTUS. Ornamental.
Euphorbia milii Moulins (Euphorbiaceae). CROWN-OF-THORNS. Ornamental.
Euphorbia tirucalli L. (Euphorbiaceae). PENCIL TREE. Ornamental.
Ixora coccinea L. (Rubiaceae). IXORA. Ornamental.
Juniperus conferta Parl. (Cupressaceae). SHORE JUNIPER. Ornamental.
Lactuca sativa L. (Asteraceae). LETTUCE. Food.
Lycopersicon esculentum (L.) Miller[1] (Solanaceae). TOMATO. Food.
Mangifera indica L. (Anacardiaceae). MANGO. For food and as an ornamental.
Manilkara zapota (L.) Royen (Sapotaceae). SAPODILLA. As an ornamental and for food.
Melicoccus bijugatus Jacq. (Sapindaceae). SPANISH LIME. Ms. Smallwood told us that two trees remained on the island until they were cut in 1974. Ornamental.
Monstera deliciosa Liebm. (Araceae). CERIMAN. Ornamental; fruit is sometimes eaten.
Musa paradisiaca var. *sapientum* Kuntze (Musaceae). BANANA. As an ornamental, rarely for food.
Mutingia calabura L. (Elaeocarpaceae). STRAWBERRY TREE. As an ornamental or as a fruit tree.
Nerium oleander L. (Apocynaceae). OLEANDER. Ornamental.
Pedilanthus tithymaloides Poit. (Euphorbiaceae). SLIPPER-FLOWER. Ornamental.
Pelargonium hortorum Bailey (Geraniaceae). GERANIUM. Ornamental.
Phaseolus vulgaris L. (Fabaceae). KIDNEY BEAN. Food.
Phoenix roebellinii O'Brien (Arecaceae). DATE PALM. Ornamental.
Phoenix rupicola T. Anderson (Arecaceae). PALM. A few of these trees were planted near the Smallwood Store by Mr. C. S. Smallwood.
Platycerium bifurcatum (Cav.) C. Chr. (Polypodiaceae). STAGHORN FERN. Ornamental.
Pleomele marginata (Lam.) N. E. Br. (Agavaceae). DRACENA. Ornamental.
Plumbago capensis Thunb. (Plumbaginaceae). LEADWORT. Ornamental.
Plumeria rubra L. (Apocynaceae). FRANGIPANI. Ornamental.
Poinsettia pulcherrima (Willd.) R. Graham (Euphorbiaceae). POINSETTIA. Ornamental.
Polyscias filicifolia (Moore) Bailey (Araliaceae). ARALIA. Ornamental.
Polyscias guilfoylei (Bull.) Bailey (Araliaceae). ARALIA. Ornamental.

[1] According to the Standing Committee on Stabilization of Specific Names (Taxon **24**(1): 174. 1975), the correct name for the tomato is *Lycopersicon lycopersicum* (L.) Karsten ex Farwell. However, Terrell (Taxon **26**(1): 129–131. 1977) comes to a different conclusion and accepts the name used by the authors of the present paper. *Ed.*

Pouteria campechiana (H.B.K.) Baehni (Sapotaceae). CANISTEL. For fruit and as an ornamental.

Prunus persica (L.) Batsch (Rosaceae). PEACH. Fruit tree.

Punica granatum L. (Punicaceae). POMEGRANATE. For fruit and as an ornamental.

Rhaphidophora aurea (Linden ex André) Birdsey (Araceae). POTHOS. Ornamental.

Ricinus communis L. (Euphorbiaceae). CASTOR BEAN. Ornamental.

Rosa sp. (Rosaceae). ROSE. Ornamental.

Roystonea regia (H.B.K.) Cook (Arecaceae). ROYAL PALM. Ornamental.

Sabal palmetto (Walter) Lodd. ex Schultes (Arecaceae). CABBAGE PALM. When the Smallwood family moved to the island in 1897, there were no palms of any kind on Chokoloskee. The largest *Sabal* on the island now is beside the Smallwood Store; C. S. Smallwood planted the tree in 1919, and it now has about ten feet of trunk. Other small palms were planted near the store by Thelma Smallwood. The palms they planted were from the mainland, where they remain abundant. Ornamental.

Sanchezia speciosa Leonard (Acanthaceae). SANCHEZIA. Ornamental.

Schinus terebinthifolius Raddi (Anacardiaceae). PEPPER TREE. Ornamental. Widely naturalized in southern Florida.

Setcreasea purpurea Boom (Commelinaceae). PURPLE QUEEN. Ornamental.

Spathodea campanulata Beauv. (Bignoniaceae). AFRICAN TULIP TREE. Ornamental.

Swietenia mahagoni Jacq. (Meliaceae). MAHOGANY. Ornamental.

Syzygium cuminii (L.) Skeels (Myrtaceae). JAMBOLAN PLUM. As an ornamental and for fruit.

Tamarindus indicus L. (Fabaceae). TAMARIND. As an ornamental and for fruit.

Tecomaria capensis (Thunb.) Spach (Bignoniaceae). CAPE HONEYSUCKLE. Ornamental.

Terminalia catappa L. (Combretaceae). TROPICAL ALMOND. Ornamental.

Thrinax radiata Lodd. ex J. A. & J. H. Schultes (Arecaceae). THATCH PALM. Said to be native to Chokoloskee, but no longer found in the wild (Read, 1975). Ornamental.

Thuja orientalis L. (Cupressaceae). ARBOR VITAE. Ornamental.

Tillandsia usneoides L. (Bromeliaceae). SPANISH MOSS. Ornamental.

Veitchia merrillii (Becc.) Moore (Arecaceae). CHRISTMAS PALM. Ornamental.

Yucca aloifolia L. (Liliaceae). SPANISH DAGGER. Ornamental.

Zea mays L. (Poaceae). CORN. Food.

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DATES OF PUBLICATION OF SARGENT'S SILVA OF NORTH AMERICA *

PAUL D. SORENSEN

FEW WHO HAVE HAD OCCASION to open its pages would disagree that the *Silva of North America*, by Charles Sargent, ranks high among the most sumptuous botanical works ever published. Its lavish format matches the generous bibliographic, descriptive, and anecdotal information it contains. Its artistic merits extend to nearly all aspects of its production including the superb quality of the line drawings by C. E. Faxon, the skill and craftsmanship of their engraving and printing, and the clarity of the type face.

Houghton, Mifflin and Company originally offered the volumes at $25 each, or $300 for the twelve volumes planned. During the eight years spanned in preparing the first twelve volumes, much additional information came to light on new species in the plant families already covered. To accommodate these new species, Sargent added a two-volume supplement, volumes 13 and 14. These also sold for $25 per volume, bringing the price for the full fourteen-volume work to $350 (Sargent, 1902–1913). The high cost (by late nineteenth century standards) required that the *Silva* depend chiefly on pre-publication subscriptions as the main manner of sale, thereby avoiding expensive inventories of unsold books. As a result the work passed out of print rather soon. It was reprinted (by a photo-offset method) in 1947 by Peter Smith of Magnolia, Massachusetts. The first reprinting was sold by the early 1960's. Mr. Smith, who still owns the copyright to the *Silva*, has told me he plans to issue another printing of the facsimile edition for release late in 1977.

Sargent's *Silva* is an important historical reference and one likely to be overlooked owing to its somewhat limited distribution. Its historical importance is based on the fact that Sargent was one of the first and most influential champions of nomenclatural priority, and the *Silva* is the first major treatise covering a large and diverse number of North American plants in which the rule of priority was strictly applied.

The *Silva* does not contain any new plant names. It includes only those species first described and published elsewhere; it does, however, resurrect many names from obscurity. Since the date when a certain name, though not new, has been recalled from earlier literature and used in place of another may be of some interest or importance, the publication date of the work where such a name reappeared could be critical. When I recently had occasion to consult the *Silva*, the edition available to me at the time was the 1947 Peter Smith facsimile reprint, in which I discovered that all

* Sargent, Charles Sprague. The Silva of North America; a description of the trees which grow naturally in North America exclusive of Mexico. Illustrated with figures and analyses drawn from nature by C. E. Faxon. 14 vols. Houghton, Mifflin and Company, Boston. 4°. *740 plates*. 1890–1902.

seven volumes (the fourteen volumes of the original bound in seven) bore the same title page which I assumed had been that of the original Volume 1. The entire work thus gave the appearance of having been published in 1890 and contradicted the sequence of issuance according to the account of Sutton (1970). In turning to the original edition for clarification on publication dates, I encountered another discrepancy: the title page of the original Volume 1 carries the date 1891, a year later than the date given in the reprint, but in this volume the copyright is dated 1890, which probably represents the source of the "1890" used on the title page of the reprint. Which is the correct date? In what year did the volume actually appear? In searching for these answers, I eventually learned that in volumes 1, 3, and 11, the title page or copyright dates disagree with the actual dates of publication. I have arrived at the determination of correct publication dates, as outlined in TABLE 1, by searching published reviews, library catalogues, and notes by Sargent as well as those of Sutton (1970), his biographer. The details of these sources appear among the notes pertaining to each volume presented below. For most of the volumes, corroboration of publication dates comes largely from Tucker (1914), *Catalogue of the Library of the Arnold Arboretum*. Here the catalogue entry (p. 623) lists exact dates for every volume except Volume 1, which is given merely as 1891. The printing of an exact date for thirteen of the fourteen volumes of the *Silva* aroused my curiosity as this practice seems not to occur elsewhere in the *Catalogue*, or, if it does, to do so inconsistently. I suspect that the exact dates indicate the dates when the volumes arrived at the library and were accessioned. One would expect accuracy from this entry inasmuch

TABLE 1. **Dates of publication of the Silva of North America by Charles Sprague Sargent.**

VOLUME NUMBER	TITLE PAGE DATE	COPYRIGHT DATE	PLATE NUMBERS	ADOPTED PUBLICATION DATE	SOURCE
1	1891	1890	1– 50	October 1, 1890	Sargent, Preface to Vol. 13
2	1891	1891	51– 97	May 23, 1891	Tucker
3	1892	1891	98–147	January 21, 1892	Tucker
4	1892	1892	148–197	July 2, 1892	Tucker
5	1893	1893	198–251	December 30, 1893	Tucker
6	1894	1894	252–300	May 18, 1894	Tucker
7	1895	1895	301–355	February 1, 1895	Tucker
8	1895	1895	356–438	September 20, 1895	Tucker
9	1896	1896	439–496	March 16, 1896	Tucker
10	1896	1896	497–537	November 28, 1896	Garden & Forest (Dec. 9) 1896
11	1897	1897	538–592	April 27, 1898	Tucker
12	1898	1898	593–620	January 10, 1898	Tucker
13	1902	1902	621–704	December 15, 1902	Tucker
14	1902	1902	705–740	December 15, 1902	Tucker

as the *Catalogue* comes from the same institution as the *Silva*. But, as I point out later, in addition to the 1891 date given for Volume 1, at least one other of the dates given by Tucker (1914) lacks accuracy. I hope that my clarifications will aid those who, as I, have been vexed by the problem of publication dates in this work.

NOTES ON THE SEPARATE VOLUMES

VOLUME 1. Magnoliaceae to Ilicineae [Aquifoliaceae]. Pp. i–ix, 1–119, *plates 1–50*.
Publication date: October 1, 1890.

In the preface to Volume 13 (the first of a two-volume supplement), Sargent (1902) gives the publication date of Volume 1 as October, 1890. Sutton (1970, p. 150) states that, "volume one of Sargent's *Silva* appeared in 1891." She probably derived this date from the title page of Volume 1 as noted above. But a page later (p. 151), she quotes from a review of the *Silva* which appeared in the January 3, 1891, issue of *Gardener's Chronicle* (anon., 1891a). It seems unlikely that a review would appear in a British periodical on the third day of the new year unless the reviewer had had the work in hand a few weeks earlier. Additional reference supporting an 1890 publication date comes from an article in *Garden and Forest* (Britton, 1890), of December 3, 1890, announcing the appearance of Volume 1.

Since Sargent himself established the date in October of that year, I propose October 1, 1890, as the day of publication.

VOLUME 2. Cyrillaceae to Sapindaceae. 117 pp., *plates 51–97*.
Publication date: May 23, 1891 (Tucker, 1914).

An unsigned review of Volume 2 of the *Silva* appeared in the June 10, 1891, issue of *Garden and Forest* (anon., 1891b). There the phrase, "The second volume of this work which has just been issued . . ." corroborates Tucker's accession date of May 23, 1891.

VOLUME 3. Anacardiaceae to Leguminosae. 141 pp., *plates 98–147*.
Publication date: January 21, 1892 (Tucker, 1914).

The words, "The third volume . . . which has recently appeared . . .," taken from a review in *Garden and Forest* dated February 17, 1892 (anon., 1892), suggest that the date provided by Tucker comes very close to the actual date of publication, and I have adopted it here.

VOLUME 4. Rosaceae to Saxifragaceae. 141 pp., *plates 148–197*.
Publication date: July 2, 1892 (Tucker, 1914).

The celebrated Liberty Hyde Bailey published a review (1892) of Volume 4 in the July 20, 1892, issue of *Garden and Forest*. The interval between the date of this review and the earlier date of Tucker as noted above argues in favor of adopting her date for the date of publication.

VOLUME 5. Hamamelidaceae to Sapotaceae. 189 pp., *plates 198–251.*
Publication date: December 30, 1893 (Tucker, 1914).

The issue of *Gardener's Chronicle* dated December 2, 1893, carries a brief notice of the appearance of Volume 5 of the *Silva* (anon., 1893a). An expanded review of this volume came out in the same periodical a week later (anon., 1893b). In neither place do we find a direct reference to a publication date. Therefore, I adopt the one given by Tucker.

VOLUME 6. Ebenaceae to Polygonaceae. 124 pp., *plates 252–300.*
Publication date: May 18, 1894 (Tucker, 1914).

A review of Volume 6 was printed in the *Gardener's Chronicle* (anon., 1894) nearly four months after the date noted by Tucker.

VOLUME 7. Lauraceae to Juglandaceae. 173 pp., *plates 301–355.*
Publication date: February 1, 1895 (Tucker, 1914).

Neither of two reviews (anon., 1895a, 1895b) reports a date of publication which would contradict that of Tucker.

VOLUME 8. Cupuliferae [Fagaceae], *Quercus*. 190 pp., *plates 356–438.*
Publication date: September 20, 1895 (Tucker, 1914).

Reviews of Volume 8 (Buchenau, 1895; anon., 1896a) are not in conflict with the date of publication assigned by Tucker.

VOLUME 9. Cupuliferae [Fagaceae] to Salicaceae. 190 pp., *plates 439–496.*
Publication date: March 16, 1896 (Tucker, 1914).

A copy of the original edition held by the combined libraries of the Arnold Arboretum and the Gray Herbarium, Harvard University, Cambridge, bears on the title page an unsigned penciled note giving the Volume 9 publication date as March 16, 1896. This is the same date Tucker has used.

Buchenau (1896) wrote a review (dated October 16, 1896) of Volume 9 for a German periodical.

VOLUME 10. Liliaceae to Coniferae [Pinaceae *sensu lato*]. 159 pp., *plates 497–537.*
Publication date: November 28, 1896 (anon., 1896b).

In a review of Volume 10 in the December 9, 1896, issue of *Garden and Forest*, I find the only precise publication date in periodical literature for any installment of the *Silva*. It happens also that among the "exact day" dates of Tucker (1914), only this one is in error. Tucker sets the date of publication as November 30. This two-day discrepancy between the date shown in *Garden and Forest* and that given by Tucker represents the evidence upon which I conclude that the dates Tucker records reflect the times of accession of these volumes to the Arnold Arboretum library.

A review of Volume 10 appeared also in *Gardener's Chronicle* of January 2, 1897 (anon., 1897a). A second and longer article (anon., 1897b) in the

same periodical further deals with Volume 10 and adds a general essay on American trees, especially as revealed in the *Silva* up to that time.

VOLUME 11. Coniferae [Pinaceae], *Pinus*. 163 pp., *plates 538–592*. Publication date: April 27, 1898 (Tucker, 1914).

In this year *Garden and Forest* ceased publication. The magazine was not an official organ of the Arnold Arboretum, but had served as a vehicle for Sargent to express his views (Sutton, 1970). Many of the unsigned articles such as the reviews cited here were actually written by Sargent (Sutton, pers. comm.).

VOLUME 12. Coniferae [Pinaceae except *Pinus*]. 144 pp., *plates 593–620*. Publication date: January 10, 1899 (Tucker, 1914).

During the years Sargent worked on the *Silva*, many new species of woody plants from North America and elsewhere came to light. These Sargent (1902–1913) collected in a two-volume folio work entitled *Trees and Shrubs*. The original covers of these volumes are bound into the copies held by the library of the Arnold Arboretum (Jamaica Plain). Printed on these covers is an advertisement for the *Silva*, accompanied by notes on the scope of the work. The advertisement announces the date of appearance of Volume 12 as January, 1899, thus substantiating the date recorded by Tucker.

VOLUME 13. Rhamnaceae to Rosaceae. 184 pp., *plates 621–704*. Publication date: December 15, 1902 (Tucker, 1914).

This is the first of the two-volume supplement to the originally planned twelve-volume work. Both volumes appeared on the same day (see below). Sargent dated the preface in the first "June 1902." The interval from June to December when Tucker recorded the December 15 date seems a reasonable time to allow for printing.

VOLUME 14. Caricaceae to Coniferae [Pinaceae]. 52 pp., *plates 705–740*. Publication date: December 15, 1902 (Tucker, 1914).

ACKNOWLEDGMENTS

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TWO NEW SPECIES AND A NEW SUBGENUS OF CYCLANTHACEAE

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A NEW SUBGENUS AND SPECIES OF DICRANOPYGIUM

IN 1954 HARLING ESTABLISHED the genus *Dicranopygium*, with 16 species, as a segregate from *Carludovica* (Harling, 1954). Subsequently, in his *Monograph of the Cyclanthaceae*, Harling (1958) recognized 44 species in this genus. He later described three more, increasing to 47 the known number of *Dicranopygium* species (Harling, 1963, 1972, 1973). In his monograph Harling also described three subgenera of *Dicranopygium*, i.e., DICRANOPYGIUM, URIBANTHUS, and GLEASONIANTHUS.

While in Panama the present writer discovered a new species of *Dicranopygium*, *D. Harlingii* G. Wilder, which exhibited a combination of features precluding placement in any of Harling's subgenera. The species is presently described and placed in its own subgenus, TOMLINSONIANTHUS.

Material of *Dicranopygium Harlingii* was collected by G. Wilder and R. Dressler on April 29, 1973, from a single population in a region called La Eneida or Altos de Pacora, east of Cerro Jefe, Panama, at an altitude of ca. 750 meters. Plants were preserved in FAA and subsequently stored in an aqueous solution of 5 percent glycerine, 50 percent ethanol.

All measurements and illustrations of *D. Harlingii* (except the illustration in FIGURE 18) are of this preserved material. After being studied, some of the specimens including the holotype were pressed and placed on deposit at the Field Museum of Natural History, Chicago, Illinois (Field Museum sheet nos. 1764553–1764555).

Aside from indicated exceptions, the description of flowering material is based solely on study of one inflorescence from the holotype (FIGURES 1–3, I). On this inflorescence all spathes were found bent outward in the manner typical of spathes on mature cyclanthaceous inflorescences, and were intact when material was collected and preserved. This inflorescence bore staminate flowers, which appeared to be at a stage just prior to anthesis (FIGURES 6–17), and expanded staminodes (FIGURES 2, 3). However, spathes were also counted on 21 additional immature inflorescences (none from the holotype) which had peduncles sufficiently expanded to enable clear distinction to be made betwen spathes and peduncle sheaths (*sensu* Harling, 1958). The description of fruiting material is based on study of eight infructescences, none from the holotype.

During investigation of the holotype, the distal portion of the studied inflorescence was severed from the basal part, as illustrated in FIGURE 2. In addition, the two most terminal spathes were removed from the peduncle, and several flowers were excised from the spadix. However, both portions of the inflorescence and all spathes were subsequently affixed to the herbarium sheet bearing the holotype.

Some preserved specimens of *Dicranopygium Harlingii* (as well as of *Ludovia Bierhorstii*) were stained either with toluidine blue or methyl green before being photographed.

In accordance with Harling's (1958) usage, the term "stigma" is herein applied to the entire upper surface of a cyclanthaceous carpel, not merely to the hair-bearing portion (stigmatic crest). Presently described taxa, like all Cyclanthaceae, produce solely unisexual flowers.

Dicranopygium subgenus **Tomlinsonianthus** G. Wilder, subg. nov.
TYPE SPECIES: *D. Harlingii* G. Wilder.

Descriptio subgeneris: receptaculum florum masculorum planum. Perianthium verum brevissimum, lobis unilateralibus in latere florum pistillatorum spectantibus positis. Stamina pauca ad multa, latrorsa et introrsa, thecis antherarum ad basim plerumque distincte divergentibus sed interdum plus minusve parallelae et approximatae. Filamentum et bulbus basalis plana atque lata. Ubi thecae divergentes, connectivum cum filamento et bulbo basali lamellam plus minusve triangularem formans.

Staminate flowers having a distinctly marked, excentrically attached pedicel (i.e., pedicel inserted on the side of the receptacle opposite the associated pistillate flower); pedicel solid; the receptacle flat; a true (*sensu* Harling, 1958), though extremely short, perianth present, its lobes unilaterally placed on the side facing the associated pistillate flower, the glanduliferous portions extremely reduced and often not outwardly visible; stamens few to many, having both lateral and introrse dehiscence (based on orientations of non-dehisced thecae), anthers with thecae usually distinctly divergent at base but occasionally more or less parallel and approximate. The filament and basal bulb broad, flattened, and not outwardly discrete from one another. Where thecae are divergent, the connective is broad and flattened; in this case connective, filament, and basal bulb jointly forming a lamella which tends to be ± triangular.

This subgenus contains one species, a species known only from the single Panamanian locality. The name TOMLINSONIANTHUS is given in honor of Dr. P. B. Tomlinson, who has undertaken numerous important investigations of the anatomy and morphology of monocotyledons, and who originally suggested this family as a subject of my research.

Dicranopygium Harlingii G. Wilder, sp. nov. FIGURES 1–18.
Holotype from material preserved in FAA (lacking collection number), collected April 29, 1973, at La Eneida, east of Cerro Jefe, Panama, *G. Wilder & R. Dressler* (F, no. 1764553).

Laminae 7–17 cm. longae, fere ad 1/2–2/3 bipartitae, segmentis lanceolatis, acuminatis. Spathae 3–4. Spadix ellipsoidea in statu florifero (in holotypo) et in statu fructifero. Flores masculi 1.6–3 mm. longi; lobi perianthii 2–4, positis unilateralibus in latere florum pistillatorum spec-

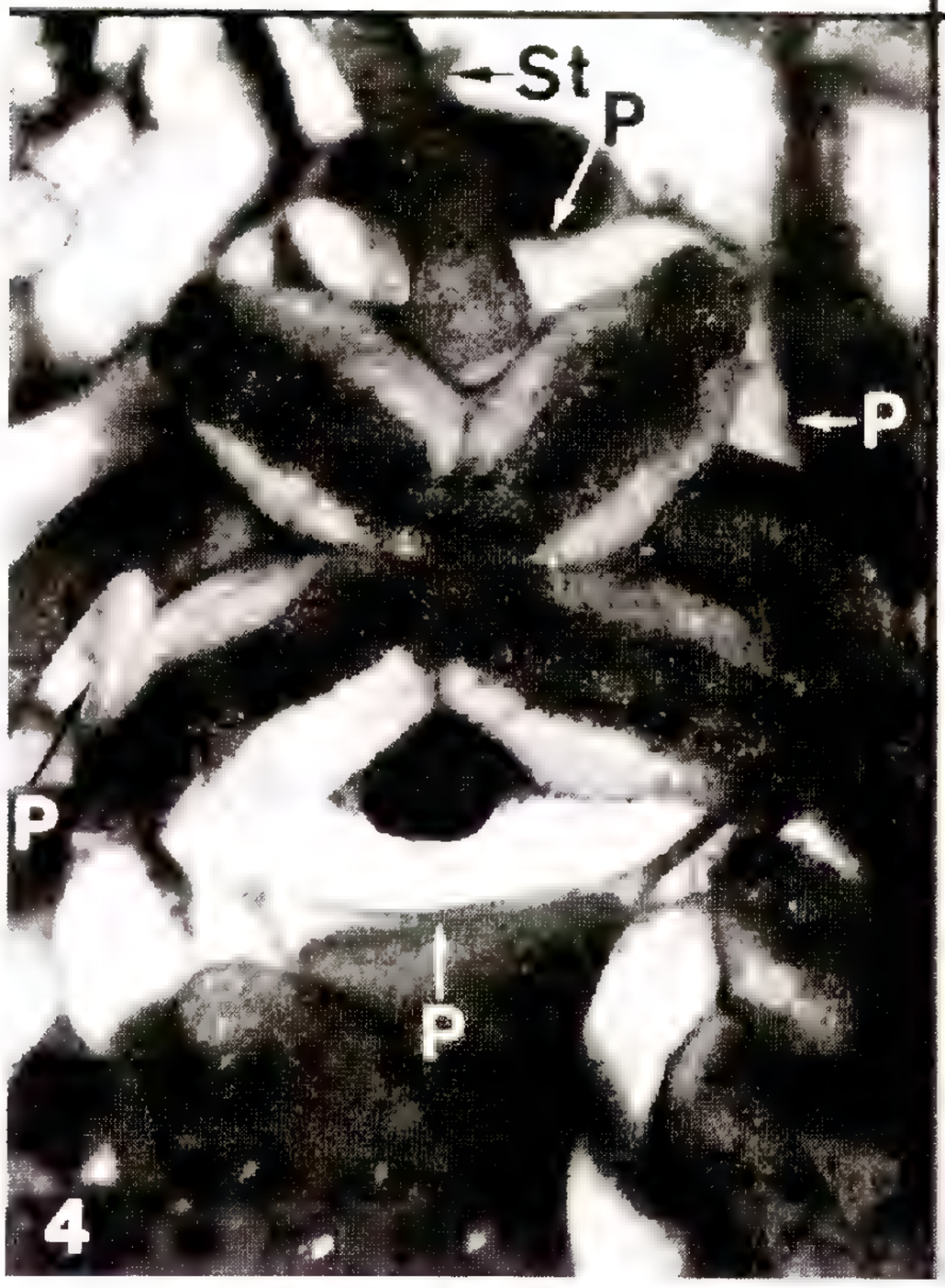
FIGURE 1. Holotype of *Dicranopygium Harlingii*, drawn from preserved specimen, × 0.5. Arrow L indicates level below which leaves had already abscissed naturally from main axis. A, B, and C are basal portions of expanding, immature vegetative branches. Numerous roots are inserted on main axis up to level of lowermost intact leaves. I, expanded inflorescence (arrow points to spadix); Ro, root; S, two lowermost spathes.

tantibus, carnosi et maxime breves. Stamina 3–14, connectivo, bulbo basali, et filamento plus minusve triangularibus. Flores feminei 3.0–3.8 mm. lati. Tepala brevissima. Stigmata sessilia, desuper visa plana ad leviter convexa, plus minusve elliptica.

Plant terrestrial and colonial. Stem up to at least 25 cm. long, 1.4 cm. in diameter. On fertile stems the leaf blades 7–17 cm. long, bifid to ca. 1/2–2/3 of their length; the segments 16–35 mm. broad, lanceolate, acuminate; petiole and leaf sheath together 3.5–8 cm. long, the margins of the sheath tearing away from the medial portion during ontogeny, this medial portion then appearing petiole-like. Peduncle of flowering specimen (holotype) 49 mm. long. Spathes 3 to 4, their basal portions white, the distal parts pigmented (at least sometimes red). On holotype 4 spathes are present: the lowermost one 32 mm. long, 15 mm. broad at base, narrowly triangular, long attenuate; the second, 29 mm. long, 22 mm. broad at base, broadly triangular, long attenuate; the third, 22 mm. long, 22 mm. broad at base, broadly ovate, cuspidate; the uppermost 17 mm. long, 18 mm. broad at base, broadly ovate, acuminate. Spadix pauciflorous, on flowering specimen (holotype) ellipsoid, 14.5 mm. long, 10 mm. wide measured to tips of staminate flowers, at least sometimes having a very short, fleshy, encircling, collar-like structure at its base, i.e., situated between the lowermost flowers and the uppermost spathe; spadix ellipsoid in fruiting stage, 9.5–21.5 mm. long, 7.5–11.5 mm. thick. Staminate flowers 1.6–3 mm. long, receptacle 0.6–1.7 mm. in diameter; perianth lobes 2 to 4, only present on the side facing the associated pistillate flower, fleshy and extremely short, rarely approaching 0.5 mm. long, varying in shape from barely raised, laterally extended ridges to triangular; stamens 3 to 14 (up to 16 in cultivated material), placed in a whorl on the receptacle margin, commonly with one to five additional stamens situated on the receptacle surface, 1.6–3 mm. long, the anthers 0.5–0.8 mm. long, each theca ca. 0.4–0.5 mm. broad, the connective, basal bulb, and filament jointly ± triangular, 0.3–1.2 mm. long, 0.5–1 mm. broad at base. Pistillate flowers 3.0–3.8 mm. broad; tepals extremely short, appearing as barely raised fleshy ridges along the edges of the flowers; stigmas sessile, seen from above virtually flat to slightly convex, more or less elliptic, the hairy portion of each stigma appearing either straight or curved when projected onto the transverse plane; staminodes ca. 3 cm. long. Seeds 0.7–0.9 mm. long, 0.25–0.3 mm. thick.

This species is named for Dr. Gunnar Harling, who has contributed very greatly to our knowledge of cyclanths in his *Monograph of the Cyclanthaceae* (1958) and other important works pertaining to the family.

Dicranopygium Harlingii clearly belongs to the genus *Dicranopygium* because it has dispersed rather than distichous foliage leaves, these having bifid, thin laminae; 3 to 4 spathes per inflorescence, these inserted immediately beneath the spadix, the two lowermost spathes ± triangular; ovaries which extend beneath the level of surrounding tissues, giving the impression that pistillate flowers are connate; four parietal placentae per



FIGURES 2–5. Material of *Dicranopygium Harlingii*: 2–4, from holotype; 5, another specimen from type locality. 2, 3, distal portion of inflorescence "I" in FIGURE 1, × 1, × 1.9, respectively. Three lowermost spathes intact when these photographs were made. Note all spathes inserted immediately below spadix. 4, pistillate flower from inflorescence in FIGURES 2 and 3, × 13. Lowermost staminode excised just above its base; only lowermost portions of remaining staminodes visible. 5, infructescence, × 3.2. Note proximity of dark-staining

ovary; perianth lobes on staminate flowers relatively reduced, never covering the stamens, and borne in one series; anthers lacking secretion globules; and terete, sculptured seeds.

Harling (1958) employed only features of staminate flowers to distinguish the three subgenera of the genus *Dicranopygium* which he recognized, i.e., DICRANOPYGIUM, URIBANTHUS, and GLEASONIANTHUS. These features are listed in the left column of TABLE 1. The four columns to the right compare his three subgenera with subgenus TOMLINSONIANTHUS according to these features.

As indicated in TABLE 1, subg. TOMLINSONIANTHUS differs from subg. DICRANOPYGIUM according to theca orientation, size and shape of connective and filament, and degree of discreteness of basal bulb; from subg. URIBANTHUS in shape of receptacle; and from subg. GLEASONIANTHUS in presence vs. absence of a "real perianth."

Harling (1958) stated that "real perianths" of the subgenera DICRANOPYGIUM and URIBANTHUS differ in two ways from the perianth type ("pseudoperianth") of subg. GLEASONIANTHUS. First, in a real perianth, the lobes have glandular tips, whereas in a pseudoperianth they never do. Second, Harling indicated that in subg. GLEASONIANTHUS perianth lobes clearly represent "metamorphosed stamens" because abnormal lobes bear rudimentary anthers at or near their tips; in contrast, he found no such evidence that real perianths of the subgenera DICRANOPYGIUM and URIBANTHUS are interpretable as staminodes.

Among staminate flowers of *Dicranopygium Harlingii* examined through the dissecting microscope at 50×, only one perianth lobe was found which appeared to have a glandular tip, i.e., a relatively large lobe below an unusual, eight-microsporangiate stamen (FIGURE 7, P; the glandular region is too small to be evident in this photograph, however). Despite the general paucity of such glandular tissue in *D. Harlingii*, the nature of the aforementioned lobe, together with the total absence of lobes having rudimentary anthers, led the present writer to conclude that *D. Harlingii* (and hence subg. TOMLINSONIANTHUS) has a "real perianth." The overall scarcity of glandular tissue in this perianth is attributed to extreme reduction of the perianth itself, a phenomenon emphasized by the minute dimensions of the perianth in comparison to those of other species of the genus *Dicranopygium*. In addition, pseudoperianth lobes on staminate flowers of subg. GLEASONIANTHUS are always extremely elongate (Harling, 1958, 1963), unlike those of *D. Harlingii*.

Because *Dicranopygium Harlingii* exhibits features in common with each of Harling's three subgenera (TABLE 1), a choice was necessitated between assigning *D. Harlingii* to a new subgenus (TOMLINSONIANTHUS), placing it in one of Harling's three subgenera, or considering its intermediate features as a basis for merging two or all of these subgenera. This writer excluded the second alternative since inclusion of *D. Harlingii* in

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spathe scars to spadix. P, tepal; S1, S2, S3, three lowermost spathes on inflorescence, numbered in acropetal order of levels of insertion on peduncle; St, staminode.

TABLE 1. A comparison of the subgenera of Dicranopygium.*

Characters of staminate flower	Subgenus DICRANOPYGIUM (41 species)	URIBANTHUS (1 species)	GLEASONIANTHUS (4 species)	TOMLINSONIANTHUS (1 species)
Occurrence of real perianth **	present	present	absent	present
Shape of receptacle of staminate flower	flat or sometimes shallowly concave	deeply hollow, funnelform	flat	flat
Type of anther dehiscence	only seldom introrse	introrse	mostly introrse	lateral and introrse (based on orientations of non-dehisced anthers)
Orientation of thecae of stamen	nearly always parallel and generally approximate	distinctly divergent at base	distinctly divergent at base	usually distinctly divergent at base but occasionally more or less parallel and approximate
Shape of connective and filament	in most species rather thin	broad and flattened	broad and flattened	filament broad and flattened, connective usually so, except when thecae are parallel and approximate
Discreteness and shape of basal bulb	distinct; globose to slightly oblong, or sometimes flattened	jointly with connective and filament forming a triangular lamella; flattened	jointly with connective and filament forming a triangular lamella; flattened	jointly with filament and usually also connective (where thecae are divergent) forming a triangular lamella; flattened

* Information on all subgenera except TOMLINSONIANTHUS is from Harling (1958, p. 275).
** See text for explanation of this term.

any of Harling's three subgenera would radically alter our concept of that subgenus, given the importance Harling (1958) placed on features characterizing each of the subgenera. The third alternative was likewise rejected since differences separating Harling's (1958) three subgenera do not appear sufficiently bridged by *D. Harlingii*. The decision to place *D. Harlingii* in its own subgenus was also influenced by Harling's (1958) conclusion that his three subgenera are ". . . well characterized and undoubtedly very natural main groups."

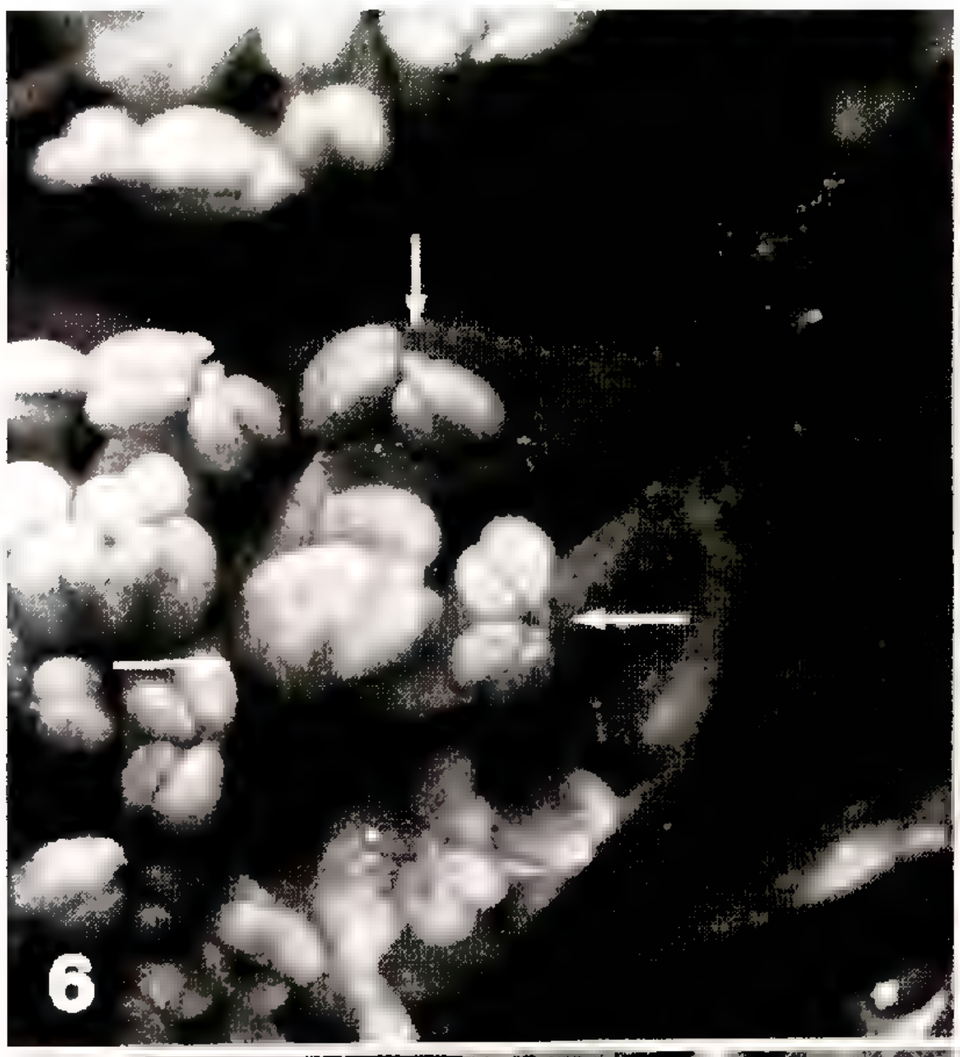
It is believed, however, that discovery of one or more additional species of the genus *Dicranopygium* which, similar to *D. Harlingii*, exhibit particular features in common with various of the subgenera, might provide sufficient justification to combine two or more of the four subgenera into one.

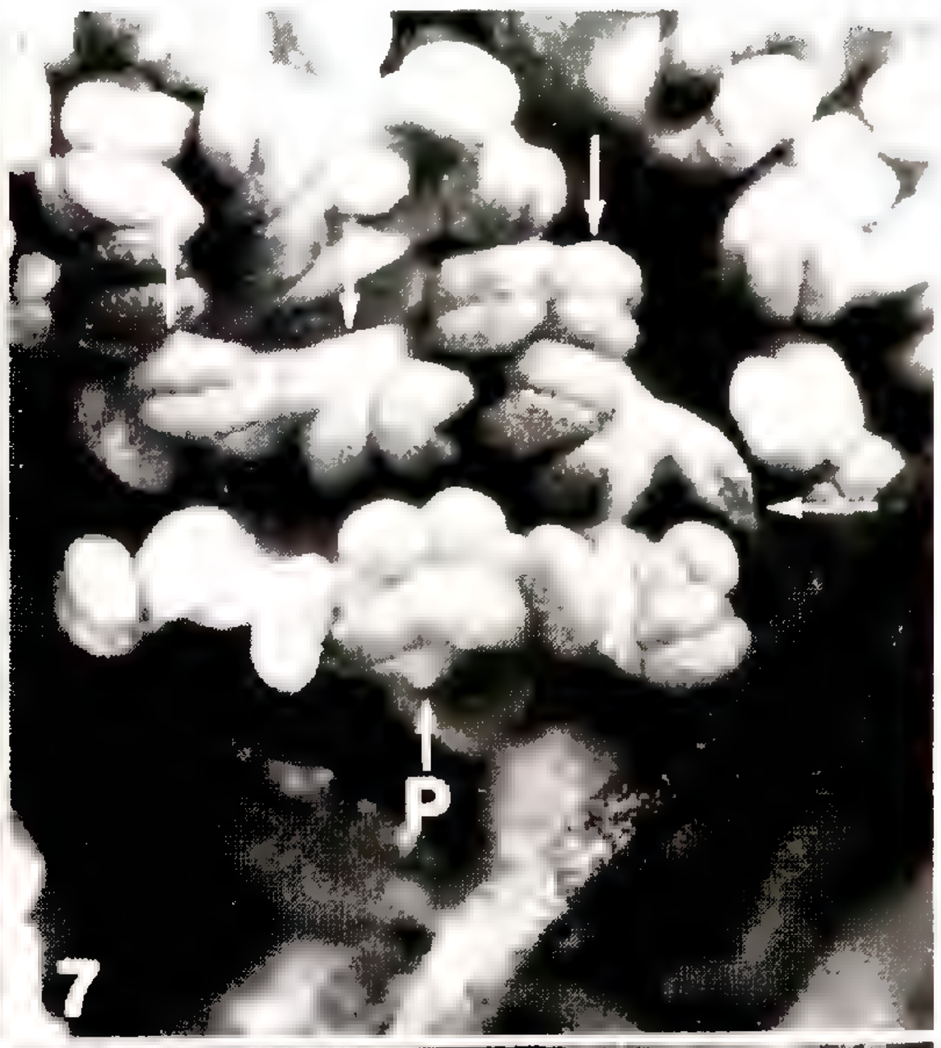
Harling (1958) stated that the most primitive of his three subgenera ". . . is certainly *Dicranopygium*, the staminate flowers of which are in all respects on a lower evolutionary level than those of the remaining groups." If he is correct, evolution of the subgenera may have proceeded as diagramed in FIGURE 19. In all subgenera other than DICRANOPYGIUM, there evolved a characteristic stamen type typically having divergent thecae and a continuous flattened lamella consisting of modified basal bulb, filament, and connective (FIGURE 19, stage A). In accordance with Harling's interpretation, there also evolved in subg. URIBANTHUS a deeply hollow, funnelform receptacle and pedicel (FIGURE 19, stage B), and in subg. GLEASONIANTHUS a "pseudoperianth" concomitant to loss of a real perianth (FIGURE 19, stage C). If we assume that the subgenera differ mainly according to the features considered, subg. TOMLINSONIANTHUS would thus differ less from subg. DICRANOPYGIUM than from either subg. URIBANTHUS or subg. GLEASONIANTHUS, and would thus represent a morphological if not a phylogenetic intermediate between DICRANOPYGIUM and the other two subgenera.

As a member of subgenus TOMLINSONIANTHUS, *Dicranopygium Harlingii* differs from all three species of the genus *Dicranopygium* described since publication of Harling's (1958) monograph, i.e., *D. Campii* Harl. (Harling, 1972), *D. macrophyllum* Harl. (Harling, 1963), and *D. robustum* Harl. (Harling, 1972). Two of these species, *D. Campii* and *D. robustum* (based on Harling's (1972) description), belong to subgenus DICRANOPYGIUM, while *D. macrophyllum* is included in subgenus GLEASONIANTHUS (Harling, 1963).

A NEW SPECIES OF LUDOVIA

In his *Monograph of the Cyclanthaceae*, Harling (1958) recognized eleven cyclanthaceous genera, but stated that only two of these genera, *Ludovia* and *Pseudoludovia*, bear consistently entire adult leaves. He recognized two species of *Ludovia* (*L. lancifolia* Brongn. and *L. integrifolia* (Woodson) Harl., described, respectively, in Brongniart (1861) and Woodson and Schery (1942)), and one of *Pseudoludovia* (*P. Andreana* Harl.,





FIGURES 6–11. Staminate flowers from holotype of *Dicranopygium Harlingii*, × 14. All flowers photographed from above while inserted on spadix. Arrows not accompanied by symbols indicate boundary of flower described in correspond-

described by Harling (1958)). No new species of these genera have been reported since publication of Harling's monograph.

The present description of *Ludovia Bierhorstii* G. Wilder is limited to one clone of this species under cultivation, although sterile plants that may belong to *L. Bierhorstii* were preserved in the field. This limitation precludes description of a mixed collection; it is necessitated by indications (detailed herein) that criteria for distinguishing between sterile plants of *Ludovia* and *Pseudoludovia* are both inadequate and suspect.

Cyclanthaceae having solely entire adult leaves and not necessarily including only *Ludovia Bierhorstii* were collected by G. Wilder and E. Hernandez between July 28–30, 1974, in Nariño, Colombia, in wet, relatively level forest situated along the north side of the road between Altaquer and Junin. In this region palms as well as other Cyclanthaceae (including species of *Asplundia*, *Cyclanthus*, *Dicranopygium*, and *Sphaeradenia*(?)) were common.

At the time of collection in 1974, it was assumed that all entire-leaved cyclanths at the collecting locality were conspecific, so no records were kept regarding specific habitats occupied by individual specimens. Because this assumption is now uncertain (for reasons to be discussed), a precise description of habitat(s) of *Ludovia Bierhorstii* cannot be provided. However, the range of habitats collectively occupied by all entire-leaved cyclanths observed at the collecting locality is described below. These plants typically grew as epiphytes on dicotyledonous trees bearing abundant bryophytes. The cyclanths were more plentiful on large, thick-stemmed trees than on small ones. Individuals situated on upright tree stems grew either upward or downward and were usually rooted at their basal ends in bryophytes and organic matter on the tree stems; their distal portions usually extended outward from the trees. However, some entire-leaved cyclanths were also found at ground level on and around a fallen tree. These plants tended to grow horizontally and upright.

Numerous specimens were preserved shortly after collection, and cuttings were also retained in living condition. Preservation was accomplished with either FAA, a formalin-ethanol solution, or 10 percent formalin, and plants were later stored in an aqueous solution of 5 percent glycerine, 50 percent ethanol. Herbarium specimens were prepared from living material

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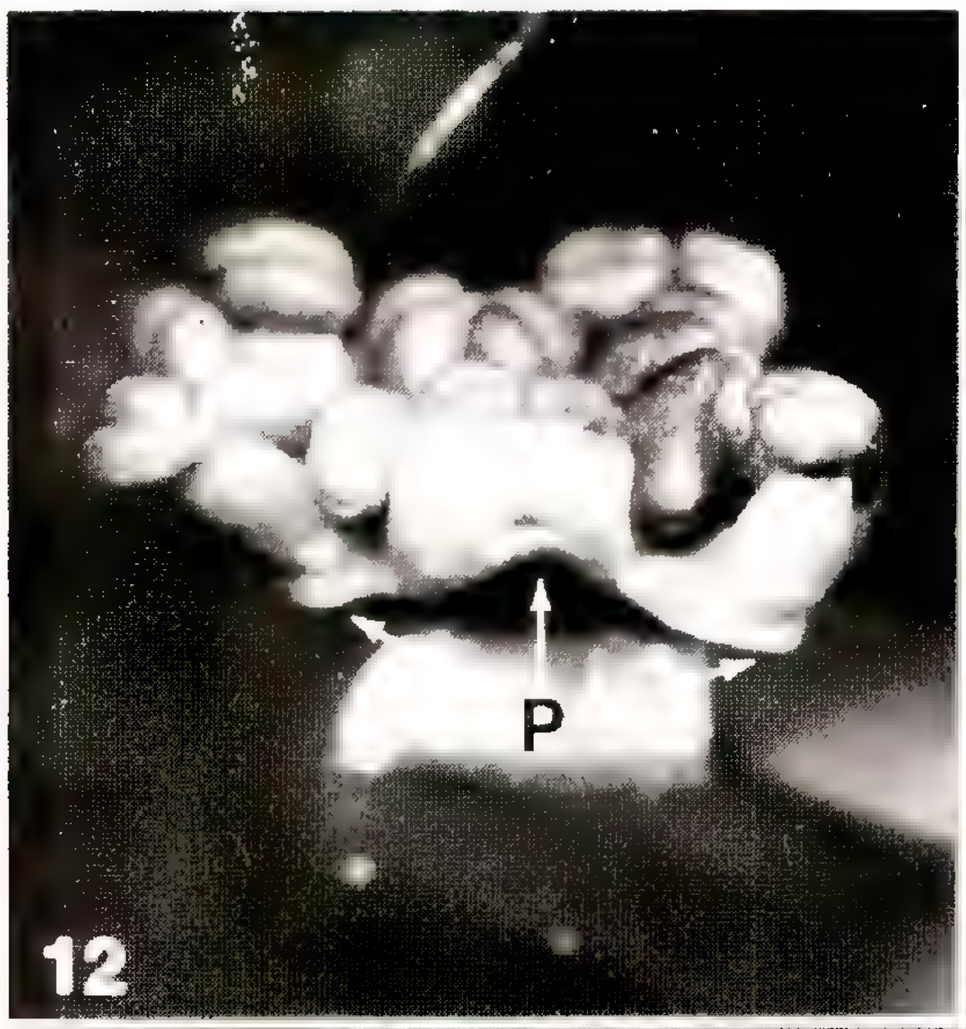
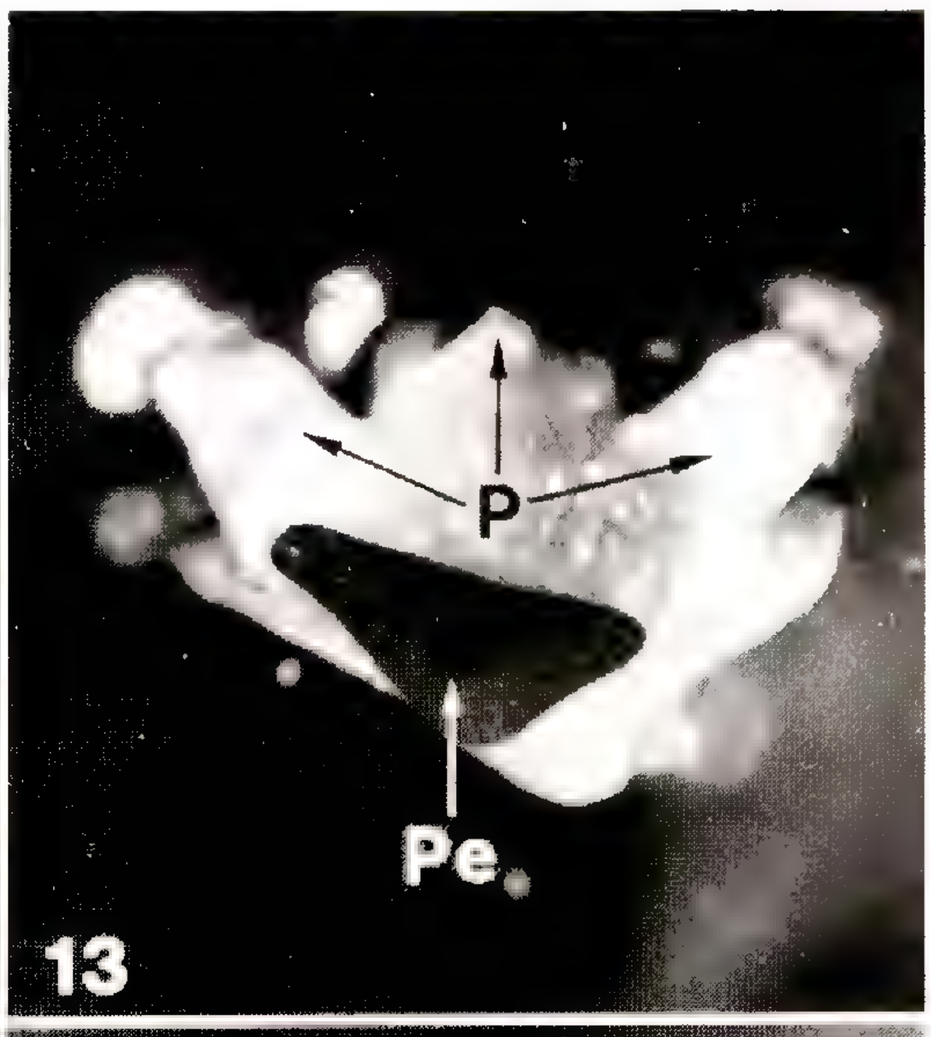
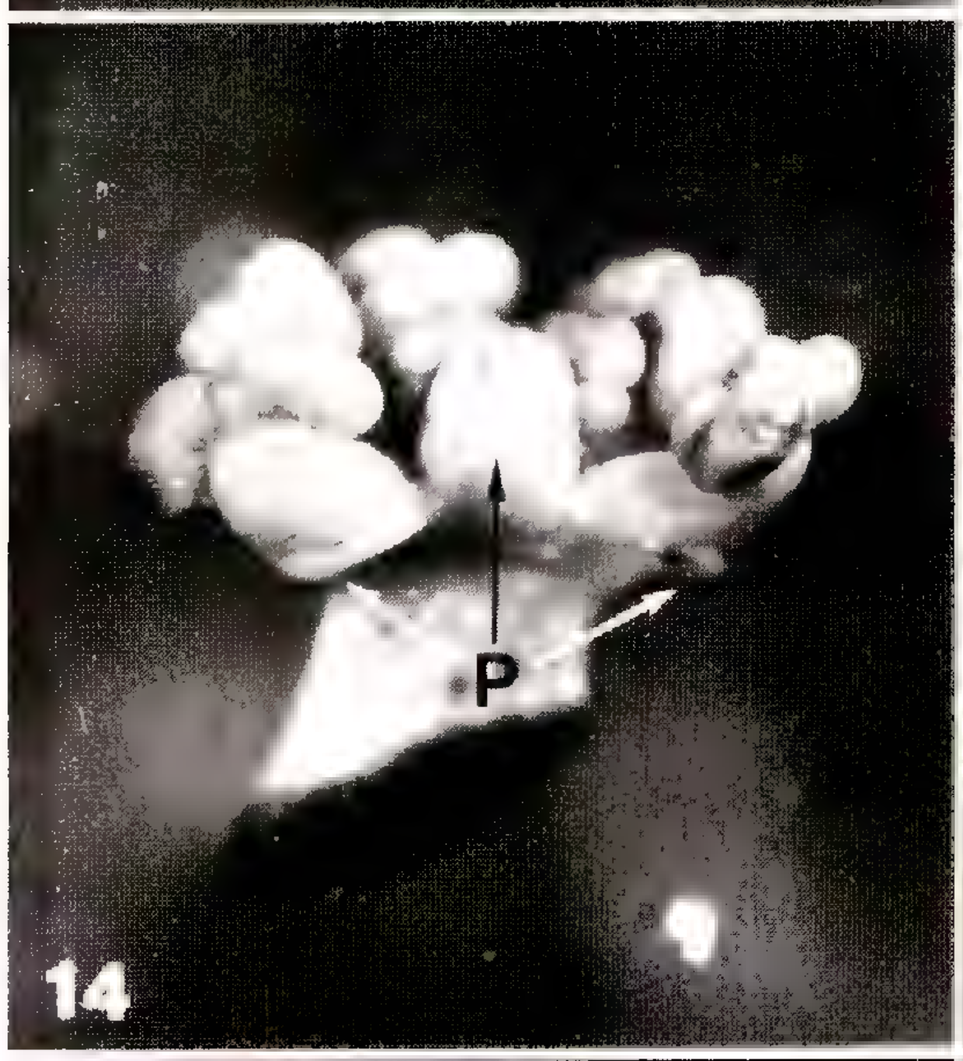
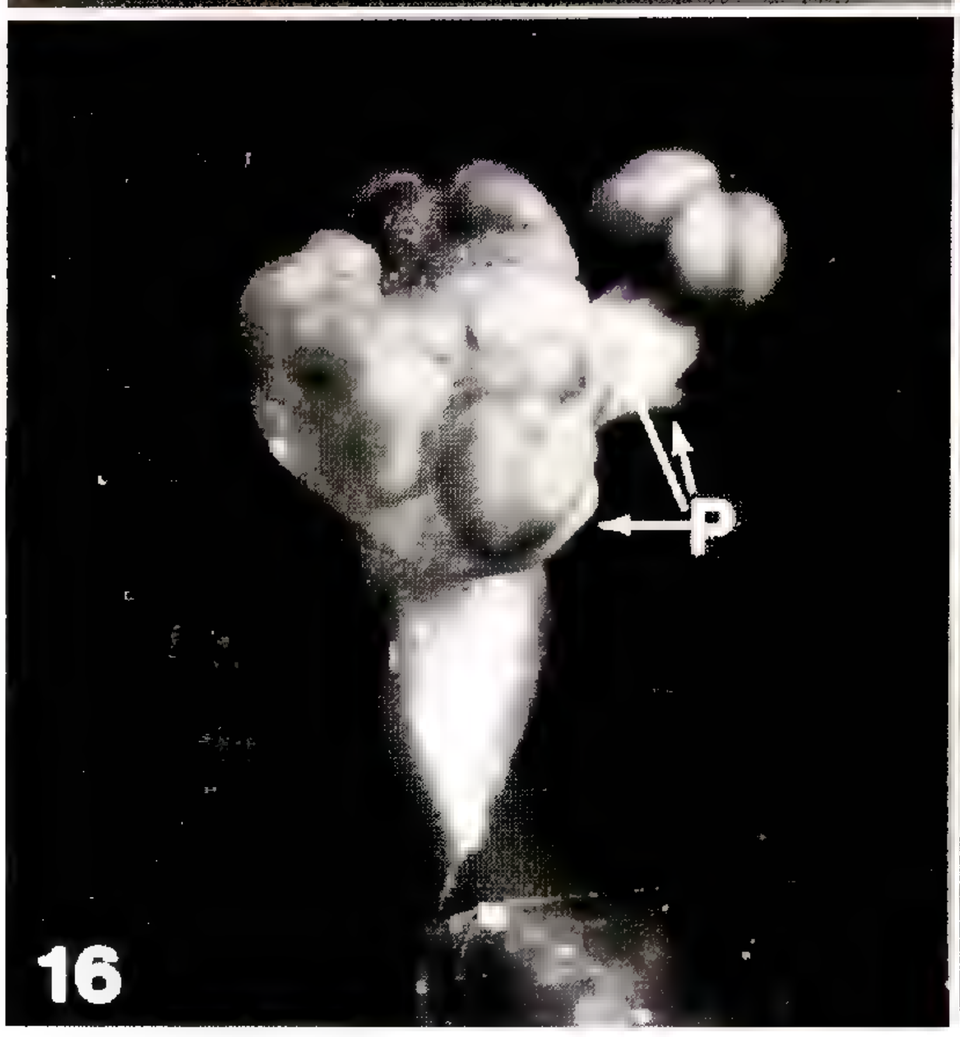
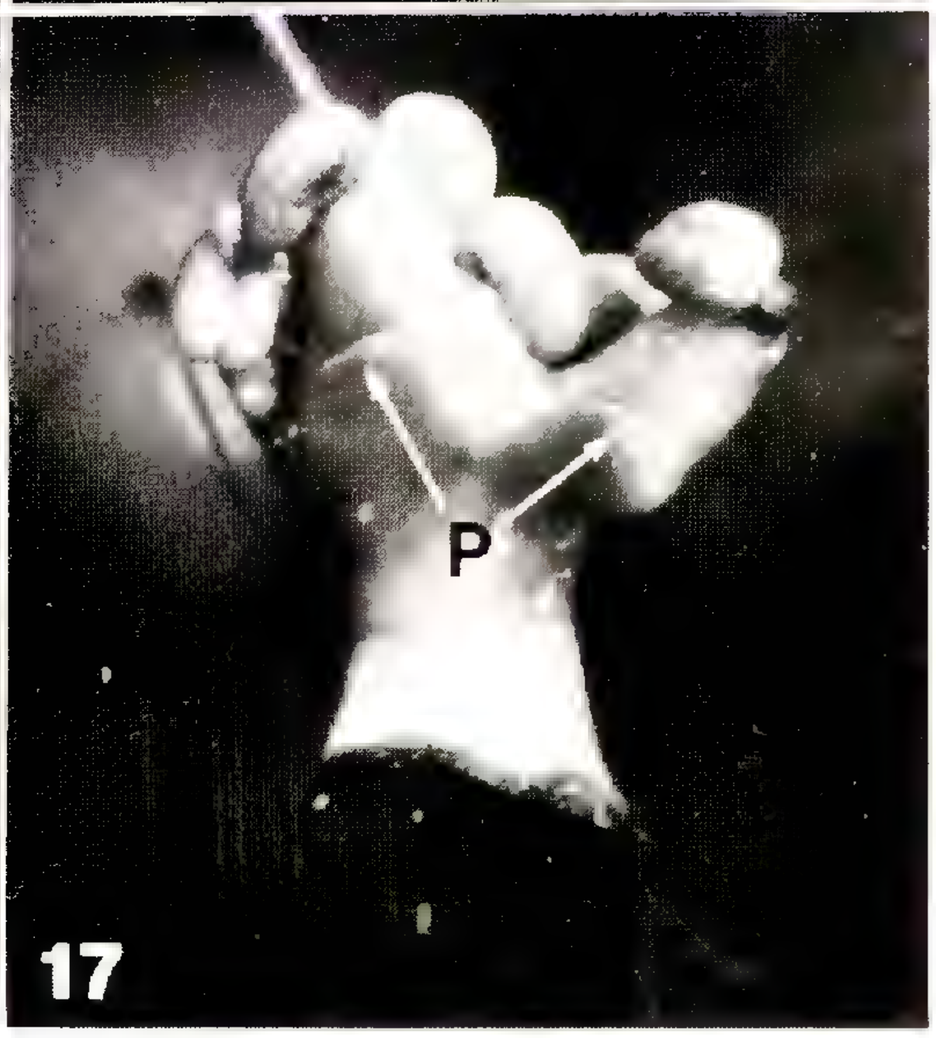
ing figure legend. 6, flower bearing three stamens, all inserted on receptacle margin. 7, flower bearing eight stamens, all on receptacle margin. Median stamen of lower three in photograph bears eight microsporangia (only four, abaxially situated, visible). This apparently single stamen may represent two connate stamens. Another stamen (indicated by arrow at right of photograph) lacks an anther apparently because of injury. Triangular perianth member beneath eight-microsporangiate stamen is largest observed in this species. Flower illustrated from side and from below, respectively, in FIGURES 12, 13. 8, flower bearing seven stamens on receptacle margin, two stamens on receptacle surface. 9, flower bearing eight stamens on receptacle margin, two on receptacle surface. Note bare portion of receptacle on right side of flower. 10, flower bearing seven stamens on receptacle margin, three on receptacle surface. 11, flower bearing nine stamens on receptacle margin, five on receptacle surface. Flower appears diamond-shaped.











FIGURES 12–17. Staminate flowers from holotype of *Dicranopygium Harlingii*, × 16. 12, 13, flower from FIGURE 7 seen from side facing associated pistillate flower (FIGURE 12); from below (FIGURE 13). Three perianth members shown, only the central one appearing triangular. Note in FIGURE 13, pedicel inserted

while near the collecting locality and also, later on, from preserved specimens. Sheets prepared at the collecting locality are on deposit at the herbarium of the Universidad de Nariño in Pasto, Colombia. Sheets prepared from sterile specimens preserved in liquid in Colombia, as well as from specimens of cultivated *Ludovia Bierhorstii* preserved in FPA, are on deposit at the Field Museum of Natural History (F).

Cuttings of entire-leaved Cyclanthaceae from the collecting locality were brought into cultivation at Fairchild Tropical Garden, Miami, Florida (This material has remained sterile and therefore cannot be identified with certainty.), and subsequently at the University of Illinois at Chicago Circle. All material at the latter institution belongs to *Ludovia Bierhorstii*.

The holotype of *Ludovia Bierhorstii* initially consisted of a leafy shoot bearing two outwardly visible inflorescences (FIGURE 20, I). However, during investigation of the holotype, the distal portion of each inflorescence was severed from the basal part. Subsequently, one of the inflorescences was completely dissected so that only one remains. On the remaining inflorescence, before preservation, the three spathes had unfolded; however, staminodes were intact and anthers had not yet dehisced. The herbarium material of the holotype exhibits this inflorescence (its staminate flowers having been largely removed from one side), its spathes, and part of the leafy shoot.

In the following description of *Ludovia Bierhorstii*, all characterizations of vegetative axes and foliage leaves (excluding measurements of maximum length of sheath, petioles, and lamina, which were done on material preserved in liquid) are based on study of living material, as is all mention of fragrance and color. In contrast, all description of structure and size of the peduncle, spadix, spathes, peduncle sheaths, flowers, and floral parts is based on specimens preserved in FPA. To avoid inclusion of obviously juvenile features, only foliage leaves 10 cm. or more long were described. With staminate flowers, measurement of receptacle diameters was made from bottom (rather than top) view of the receptacles, since this method was more accurate.

During this investigation the writer studied one inflorescence each of *Ludovia lancifolia* and *L. integrifolia* for comparative purposes. Obtained, respectively, from plants cultivated at Fairchild Tropical Garden and the University of Illinois at Chicago Circle, both inflorescences, preserved in liquid, were at anthesis. The cultivated plants of *L. integrifolia* were originally collected as cuttings by R. Dressler and G. Wilder between mid-April and early May, 1973, near the El Llano-Cartí highway, from 8 to 20 km. north of El Llano, prov. Panamá, Panama.

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on side of receptacle opposite perianth (therefore also opposite associated pistillate flower). 14–16, flower seen from side facing associated pistillate flower (FIGURE 14), from opposite side (FIGURE 15), and from side perpendicular to the other two (FIGURE 16). Flower resembles that in FIGURES 12 and 13 but lacks teratological stamens; it bears three tepals, visible only in FIGURES 14 and 16. 17, flower viewed from side facing associated pistillate flower, bearing only two tepals. P, perianth member. Pe, pedicel.

FIGURE 18. *Dicranopygium Harlingii* at the type locality. Plants of this species, indicated by arrows, growing in dried-up creek bed amidst boulders, logs, and fallen leaves.

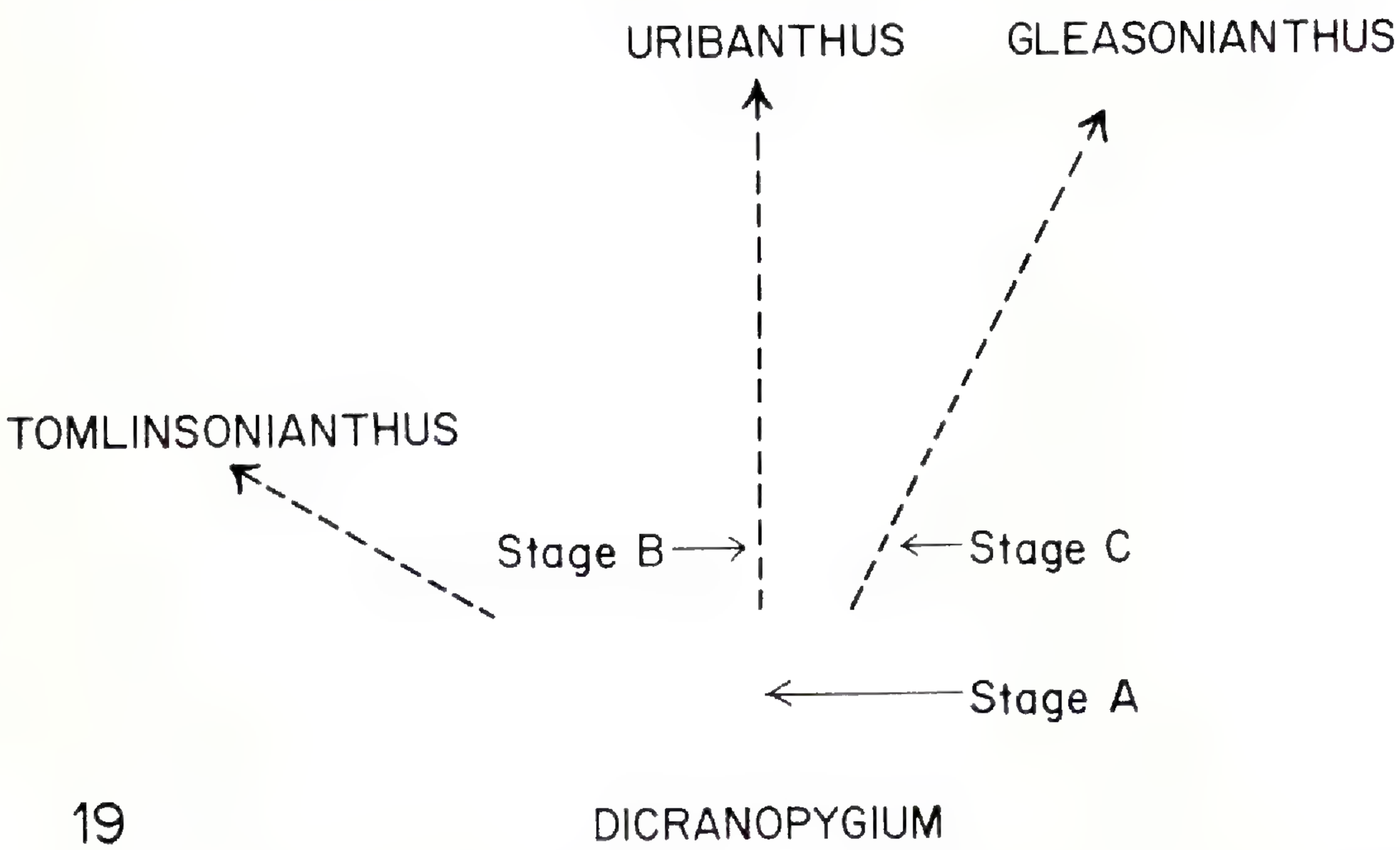


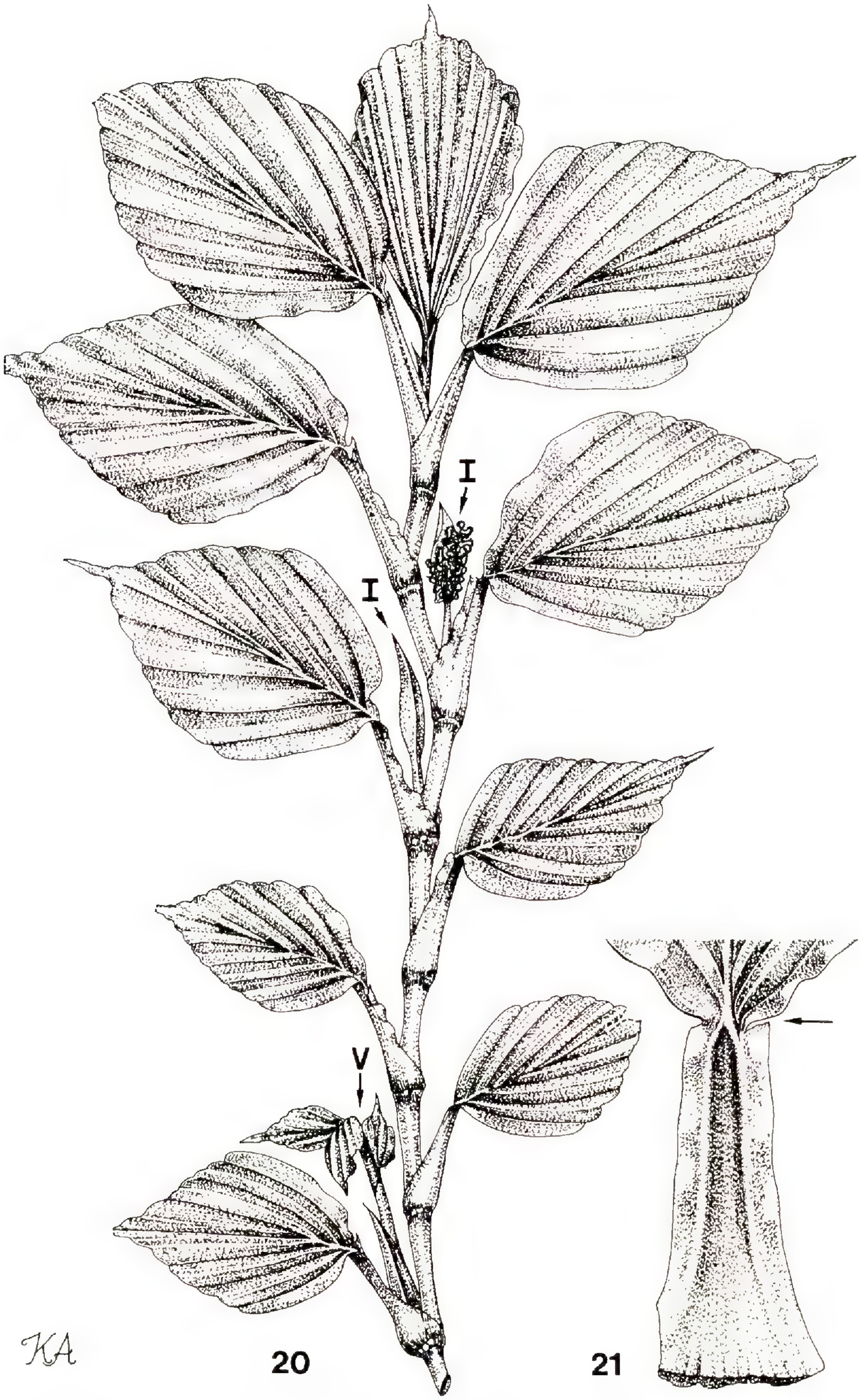
FIGURE 19. Diagrammatic representation of putative phylogeny of subgenera of *Dicranopygium*.

Ludovia Bierhorstii G. Wilder, sp. nov. FIGURES 20–44.

Holotype from cultivated material (lacking collection number) preserved in FPA, originally collected July 28–30, 1974, near Altaquer, Colombia, *G. Wilder & E. Hernandez* (F, no. 1764556).

Laminae 10–27 cm. longae, 5.5–18 cm. latae, majores late ovatae et obovatae ad plus minusve rhombicas, distincte longocuspidatae. Spathae 3, affixae ad sextam partem superam (plerumque ad decimam partem superam) pedunculi. Spadix in statu florifero anguste cylindricus, ad apices florum masculorum mensus 14–36 mm. longus et 8–11 mm. crassus, 4.5–6 mm. crassus, non flores masculi includentes. Flores masculi 3–3.5 mm. longi; receptaculum planum, infra visa orbiculare, vel aliquantum elongatum; lobi perianthii breves acuminati ad apiculatos. Stamina 36–100+; bulbis basalibus staminum marginalium in aspectu abaxiali plerumque obovatis ad obovato-depressos, plus minusve obcordatis, desuper visis radialiter ad tangentialiter complanatos; bulbis basalibus staminum centralium brevior et tenuior, sinu distali absenti, desuper visis tangentialiter complanatis ad circulares. Flores feminei in statu florifero 5.5–8.5 mm. longi, 2.7–3.5 mm. lati; tepala brevissima; stigmata (in floribus tetracarpellis) ovata, rhombica ad elliptica.

Stem at least 60 cm. long, 8.5–18 mm. in diameter, varying from reddish green to dark red (depending on concentration of small red flecks on a green background); the internodes elongate, ca. 6–9 cm. long. Leaf blades 10–27 cm. long, 5.5–18 cm. broad, the larger ones broadly ovate and obovate to ± rhombic, distinctly long-cuspidate. Sublaminar portion of leaf 5–11.8 cm. long, typically consisting entirely of leaf sheath, sometimes also exhibiting a petiole up to 4 mm. long, this petiole with two



FIGURES 20, 21. *Ludovia Bierhorstii*. 20, holotype prior to removal of the two inflorescences, × 0.20. Foliage leaves shown with adaxial sides outermost. Upper inflorescence has begun to unfold; lower one with all spathes intact. 21, adaxial view of basal portion of leaf subtending lower inflorescence in FIGURE

ridges, each ridge comprising one margin of the adaxial surface; if petiole is absent, the membranous margins of the leaf sheath continuous with margins of the lamina and sometimes red-tinged; each margin of the sheath commonly ending distally in a small lobe ca. 1–6 mm. high. Inflorescence fragrant at anthesis. Peduncle during anthesis 34–77 mm. long, light to dark green, bearing one or two peduncle sheaths. The lowermost peduncle sheath (i.e., the prophyll) relatively short and greenish white on the outside, the next higher one longer and green on the outside. Spathes 3, all inserted on the upper 15 percent (commonly upper 10 percent) of the peduncle, each one partly enveloping the spadix; the lowermost one 59–82 mm. long, 21–28 mm. broad, lanceolate, cymbiform, terminating in a rudimentary, plicate lamina, ± acute, fleshy, on the outside having a laterally extended green band on its basal-most part, the lower half mainly light brown or yellow-brown, the upper half yellow-brown or mainly exhibiting green spots on a yellow background, white or brown and brownish white on the inside, the next higher spathe 55–70 mm. long, 23–30 mm. broad, ovate, cymbiform, terminating in a ± obvious, rudimentary, plicate lamina, acuminate, somewhat fleshy, on the outside having a laterally extended green band on its basal-most part, the lower part (including the majority of this spathe) mostly light brown or yellow-brown, the upper part light brown, yellow-brown, or mainly yellow, white on the inside; the uppermost spathe 46–59 mm. long, 24–29 mm. broad, ovate, cymbiform, shortly subcuspidate, rather membranous, on the outside having a laterally extended green band on its basal-most part, otherwise light brown, white on the inside. Spadix narrowly cylindrical at anthesis, measured to the ends of the staminate flowers 14–36 mm. long, 8–11 mm. thick, when not including the staminate flowers 4.5–6 mm. thick. Staminate flowers 3–3.5 mm. long; their pedicels glistening white and of two general types, the first type belonging to staminate flowers inserted lateral to their associated pistillate flowers (relative to the long axis of the inflorescence), each such pedicel being compressed parallel to the lateral margin of the associated pistillate flower, the surfaces of this pedicel which face toward and away from the pistillate flower being, respectively, gently concave and convex, this pedicel terminating basally in a gently curved ridge (FIGURE 29), the second type of pedicel belonging to staminate flowers inserted distally or basally with respect to their associated pistillate flowers, each such pedicel typically less compressed (and then generally parallel to the radius of the associated pistillate flower) or not so, the surfaces of this pedicel which face toward and away from the pistillate flower generally being, respectively, pronouncedly concave and convex at their basal ends, the pedicel generally terminating basally in a ± distinct V-shaped ridge which opens toward the pistillate flower (FIGURES 26, 28); receptacle flat, orbicular as seen from below, 2–2.5 mm. in diameter, or somewhat lengthened, 3–5.5 × 2–3 mm.; perianth lobes white to transparent, secreting a clear,

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20, sheath appearing artificially flattened here; petiole absent (arrow indicates boundary between lamina and sheath), × 0.49. I, inflorescence; V, vegetative branch.

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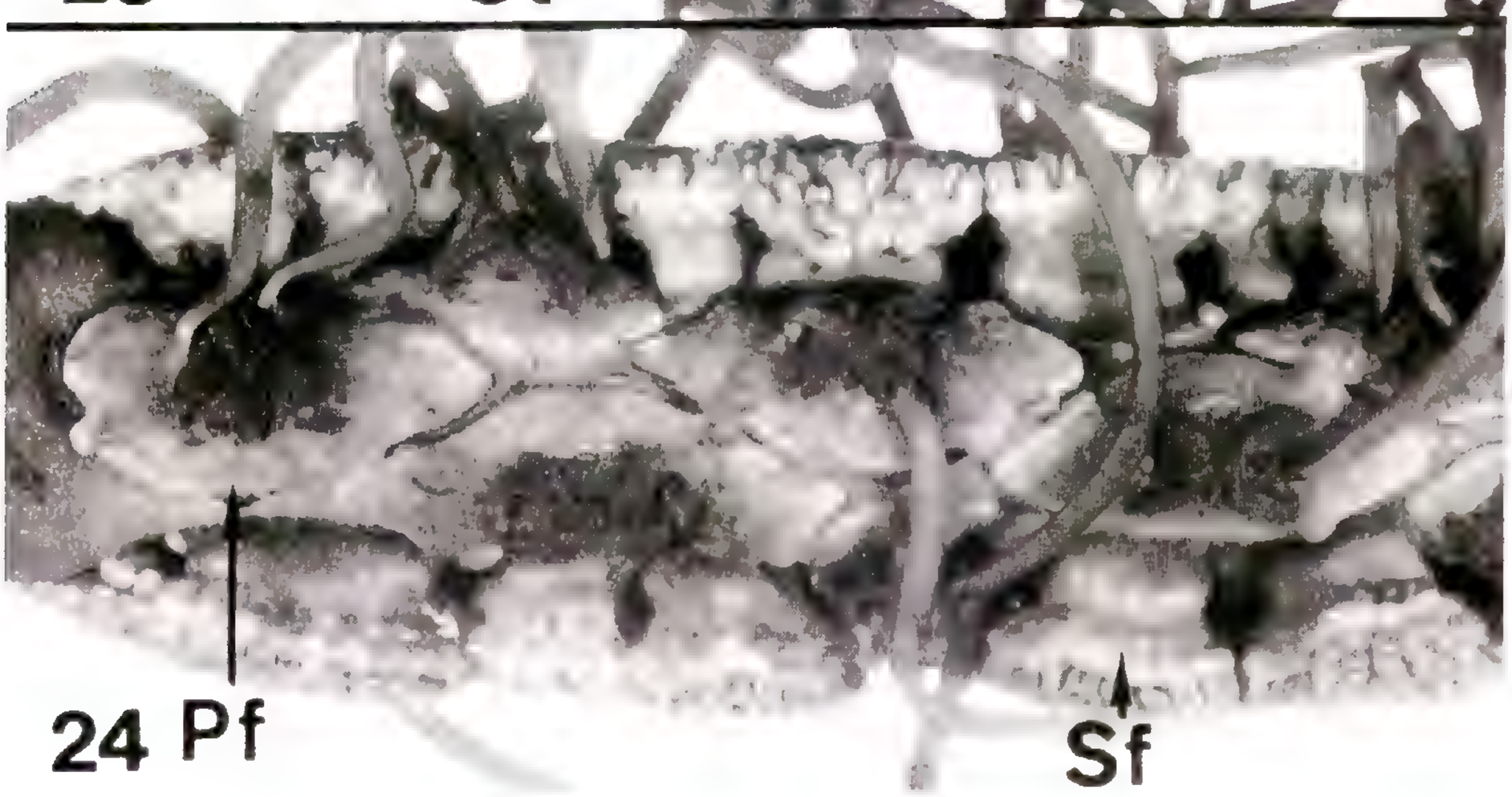

FIGURES 22–24. Distal portion of remaining inflorescence from holotype of *Ludovia Bierhorstii*. 22, 23, portion of inflorescence with all flowers intact, × 0.78, × 3.7, respectively. Note proximity of all three spathe scars to spadix. 24, portion of spadix from which staminate flowers have been dissected away,

very viscous, sticky substance, 0.5–0.7 mm. long, 0.3–0.7 mm. broad, short, acuminate to apiculate, reaching or virtually reaching the basal bulbs of the stamens, in side view each basal bulb appearing entirely exposed or mainly so; stamens 36 to over 100 although usually well within these limits, densely crowded, the most centrally situated ones differing substantially in form from those at the margin; anthers yellow, those of marginal stamens 0.5–0.7 mm. long, 0.3–0.6 mm. broad, those of the most centrally situated stamens 0.7–0.8 mm. long, 0.5 mm. broad; filaments dull white, those of marginal stamens tending to be virtually absent or extremely short, typically not reaching the maximum length of 0.2 mm., filaments of the most centrally situated stamens always obvious, ca. 0.1–0.2 mm. long; basal bulbs dull white, those of marginal stamens in abaxial view tending to appear obovate to depressed obovate, ± obcordate, in top view varying from radially to tangentially flattened, basal bulbs of the most centrally situated stamens much shorter and less thick, lacking a distal sinus, in top view appearing tangentially flattened to circular. Pistillate flowers during anthesis 5.5–8.5 mm. long, 2.7–3.5 mm. broad; tepals green basally, white distally, very short, consisting (together with the light green, more peripherally situated tissue of the same flower) of numerous closely packed, glandular(?) protuberances, the apices of these tepals thus variable, e.g., distinctly trilobed or bilobed, emarginate, or truncate, pressed against the stigmas; stigmas light green except for the hairy, white stigmatic crests, commonly 4, sometimes 5 and (by branching of one stigma) 6, somewhat laterally compressed, tending to be distinctly uncinate, seen from above (on tetracarpellate flowers) varying from ovate, or rhombic, to elliptic, projecting between the tepals; staminodes ca. 8–12 cm. long, white. Fruit and seeds unknown.

Ludovia Bierhorstii is named for Dr. David William Bierhorst, who has contributed greatly to our knowledge of anatomy and morphology of vascular plants.

Ludovia Bierhorstii clearly belongs to the genus *Ludovia* because it has larger leaves which are entire, unicostate, distichously arranged, distally crenellated, and cuspidate; a peduncle less than 12 cm. long; three spathes per peduncle, these distichously arranged, each lanceolate or ovate; a cylindrical spadix; on staminate flowers large numbers of evenly distributed, glanduliferous perianth lobes; on pistillate flowers extremely small perianth lobes; stigmas commonly uncinate, lacking styles; ovaries extending beneath the level of surrounding tissues, giving the impression of connate pistillate flowers; four parietal placentae per ovary which approach but do not reach its basal-most part.

However, *Ludovia Bierhorstii* exhibits the following features which do not conform to Harling's (1958) circumscription of *Ludovia*: the unfolded, larger leaves are somewhat plicate (FIGURE 20), the spathes are rather

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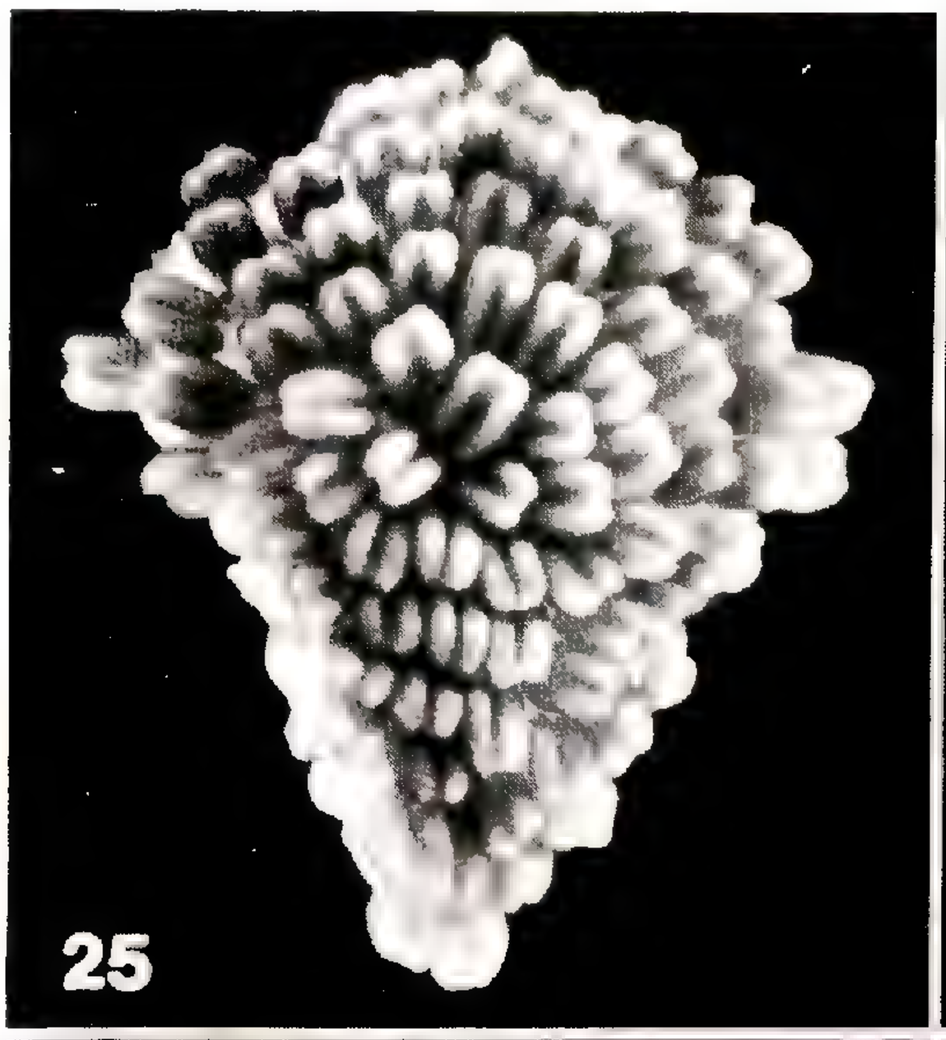
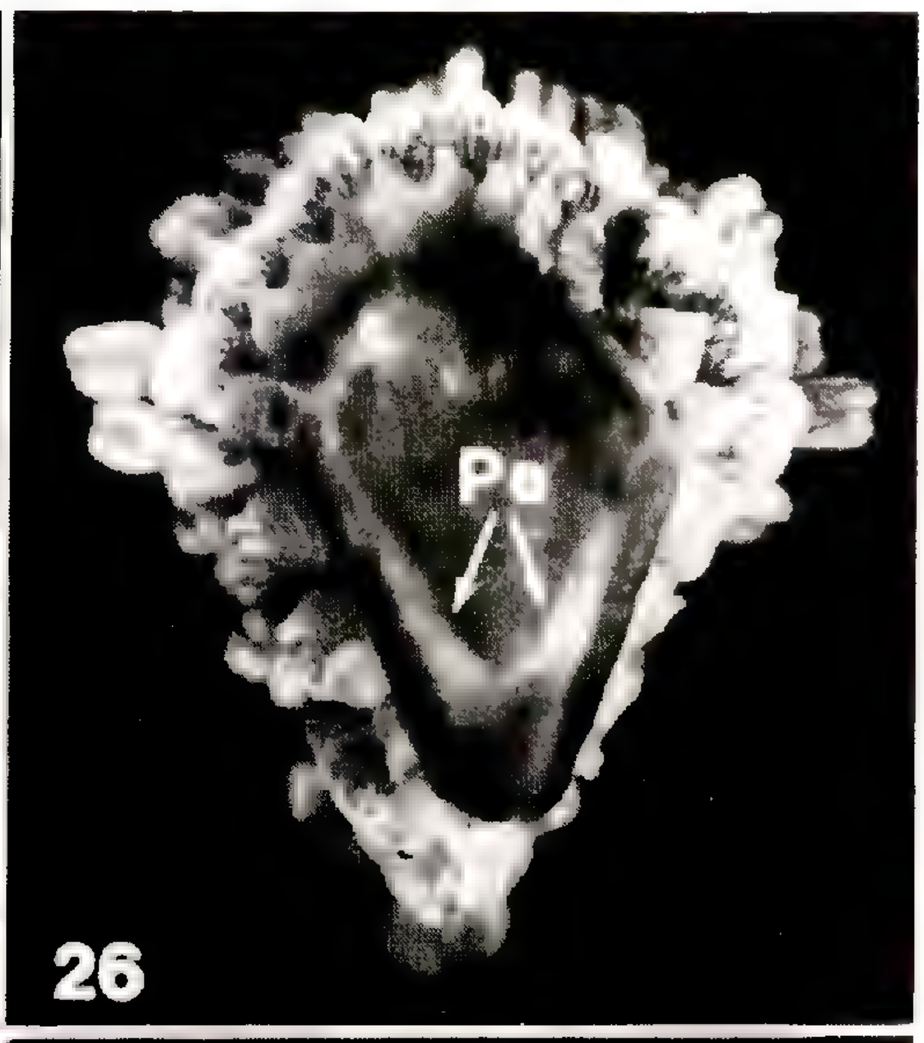
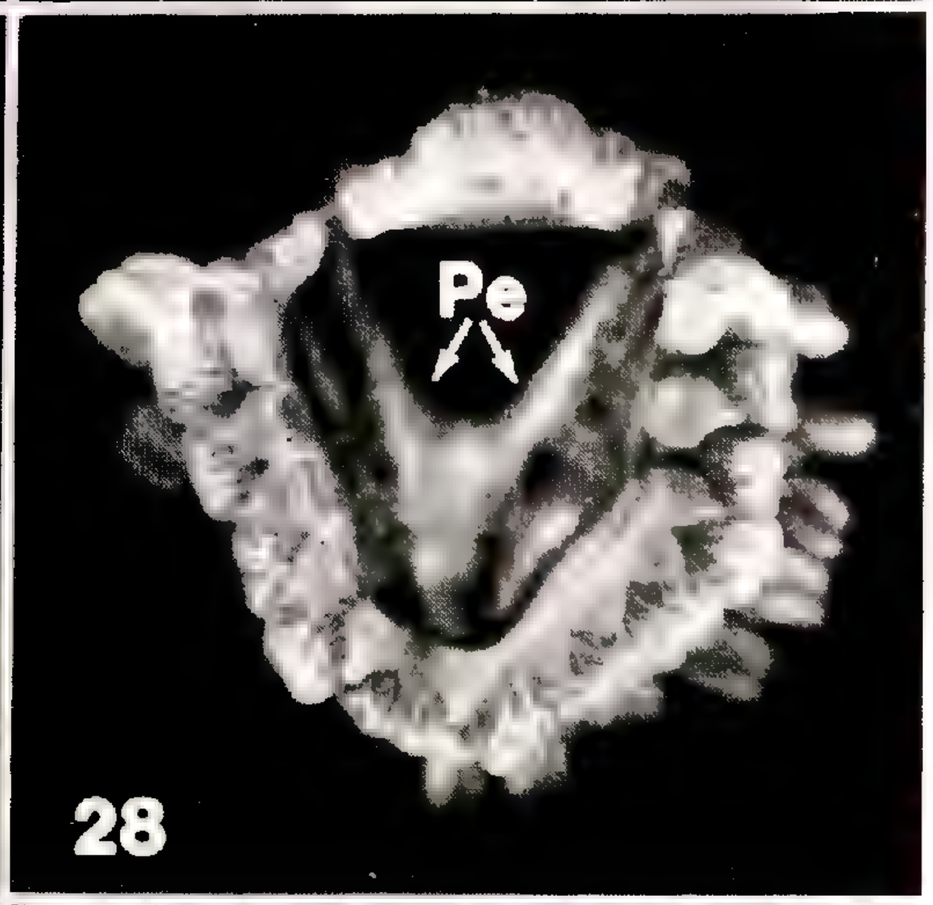
revealing pistillate flowers, × 4.2. Long axis of each pistillate flower parallels long axis of inflorescence. Pf, pistillate flower; S, spathe scars; Sf, staminate flower; St, staminode.







FIGURES 25–30. Staminate flowers from inflorescence illustrated in FIGURES 22–24, × 9.9. 25, 26, staminate flower, bilaterally symmetrical, from above (FIGURE 25) and below (FIGURE 26). 27, 28, staminate flower, more or less orbicular, from above (FIGURE 27) and below (FIGURE 28). 29, 30, two staminate

crowded beneath the base of the spadix, in examples studied being confined to the upper 15 percent (commonly, the upper 10 percent) of the peduncle. In contrast, Harling (1958) stated that for both *L. lancifolia* and *L. integrifolia*, the lowermost spathe is ". . . placed at about the middle of the peduncle." Additionally, in *L. Bierhorstii* each spathe partly encloses the spadix, although Harling (1958) indicated that in both other species of *Ludovia* the lowermost spathe does not enclose the spadix.

In the following account, except where specified, all characterizations of *Ludovia lancifolia* and *L. integrifolia* are based on Harling's (1958) descriptions of these species. Apparent differences in size between each of these species and *L. Bierhorstii* are not indicated where it is suspected that these differences may merely reflect differences in the ways the materials were preserved. Specifically, Harling (1958) apparently made some if not all of his measurements on dried specimens, while the present writer utilized solely materials which were living or preserved in liquid. Accordingly, present measurements would appear to be less reflective of shrinkage than were those of Harling (1958).

Ludovia Bierhorstii differs from *L. lancifolia* as follows:

(1) Maximum lengths of laminae in *L. Bierhorstii* and *L. lancifolia* are, respectively, 27 cm. and 110 cm. Even the largest leaf observed which might belong to *L. Bierhorstii* (an unidentifiable specimen preserved at the type locality) measured only 43 cm. long. However, in *L. Bierhorstii* and *L. lancifolia* maximum leaf diameters are comparable (respectively, 18 cm. vs. 16 cm.). In addition, foliage leaves of *L. lancifolia* differ in shape from those of *L. Bierhorstii*.

(2) During anthesis spadices of *L. Bierhorstii* and *L. lancifolia* are, respectively, 4.5–6 mm. and 12–16 mm. thick.

(3) On staminate flowers of *L. Bierhorstii* and *L. lancifolia*, receptacles are, respectively, flat vs. distinctly and broadly concave.[1]

(4) In *L. Bierhorstii* perianth lobes on staminate flowers are 0.5–0.7 mm. long and in side view fail substantially to cover basal bulbs of the marginal stamens (FIGURES 35–37). However, in *L. lancifolia*, the lobes are larger (0.8–1 mm. long), in side view substantially covering basal bulbs of the marginal stamens (based on Harling's *fig. 89a* as well as on present observation of *L. lancifolia*).

[1] Apparent contradictions exist in literature regarding *Ludovia lancifolia*. Harling (1958) described the staminate flower of *L. lancifolia* as having a ". . . receptacle distinctly and broadly concave . . . ," a feature verified during my own studies. Brongniart (1861, *fig. 4*), however, illustrated a longitudinally sectioned flower, purportedly of *L. lancifolia*, which exhibited an apparently flat receptacle. In addition, Brongniart emphasized that pistillate flowers of *L. lancifolia* lack sepals ("calyx nullus"), yet his illustration of a pistillate flower depicts what appear to be four rather well-defined tepals (Brongniart, 1861, *fig. 3*). Furthermore, Brongniart's (1861) *fig. 3* does not depict the obvious broad peripheral region of protuberances which occurs on pistillate flowers of *L. lancifolia*.

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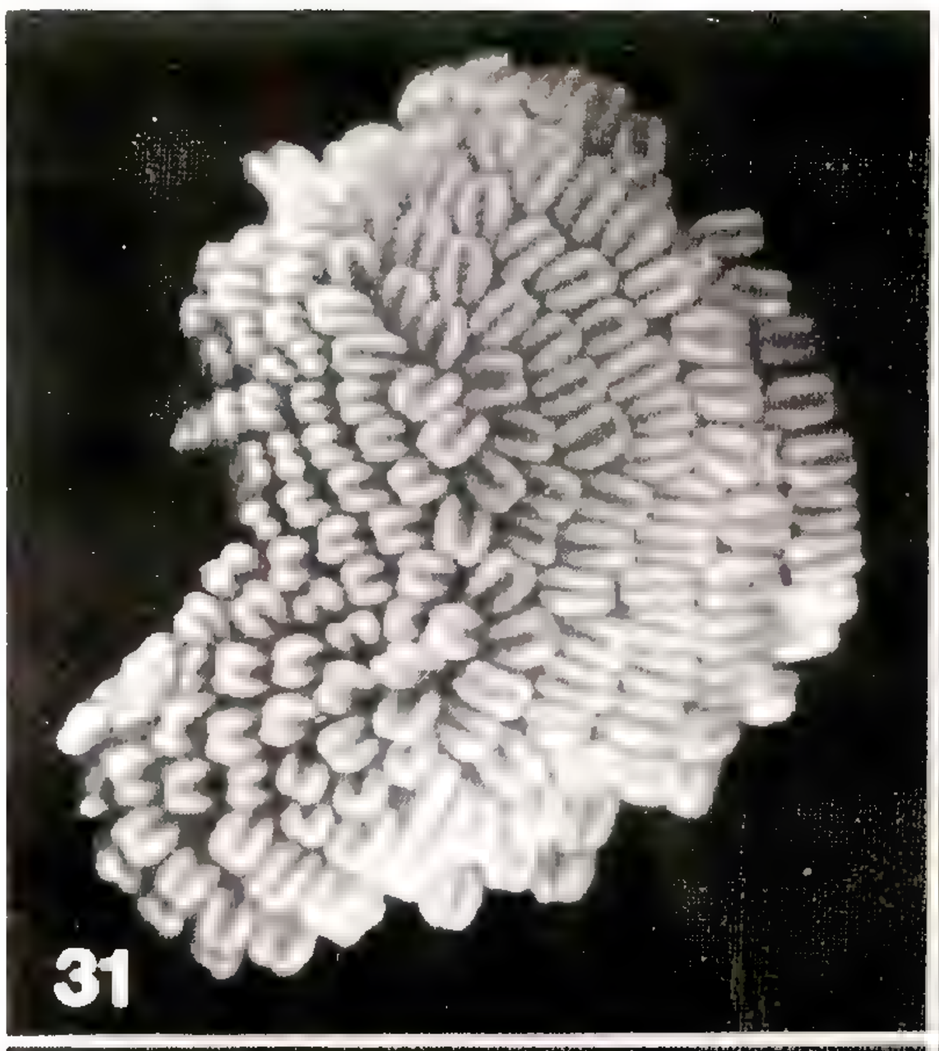
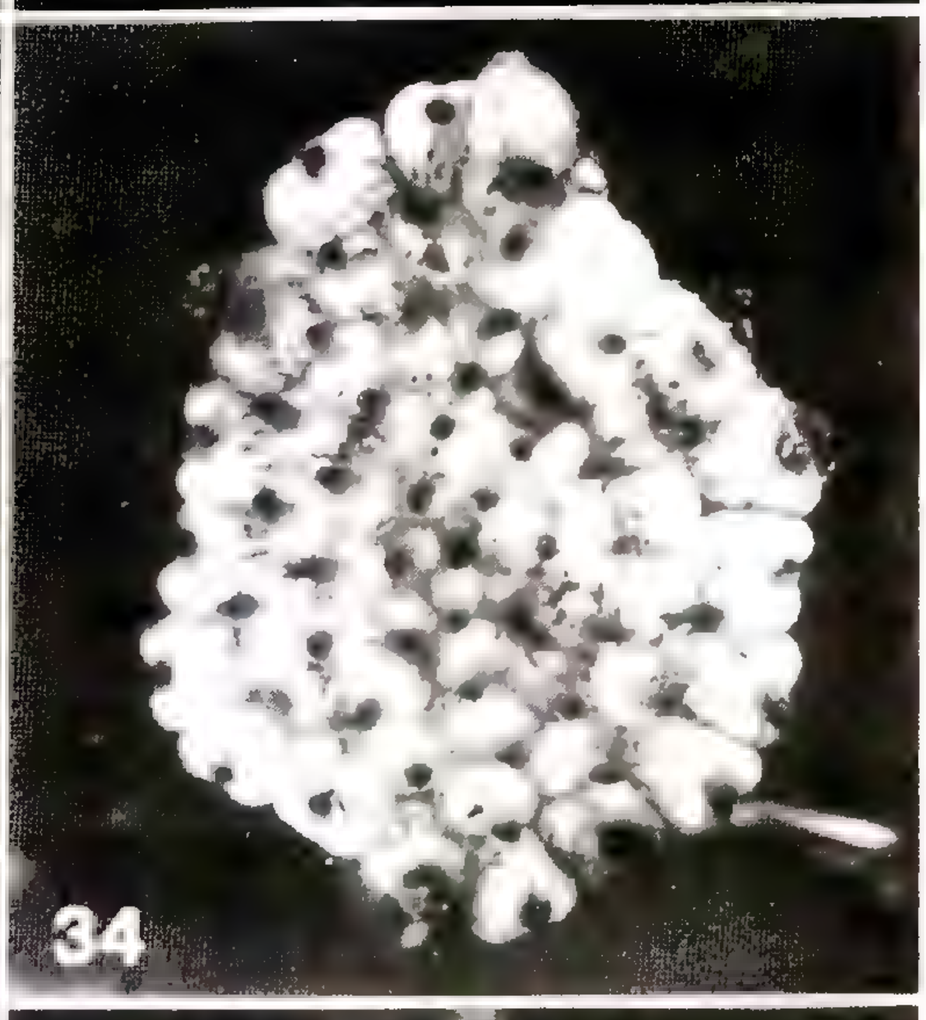
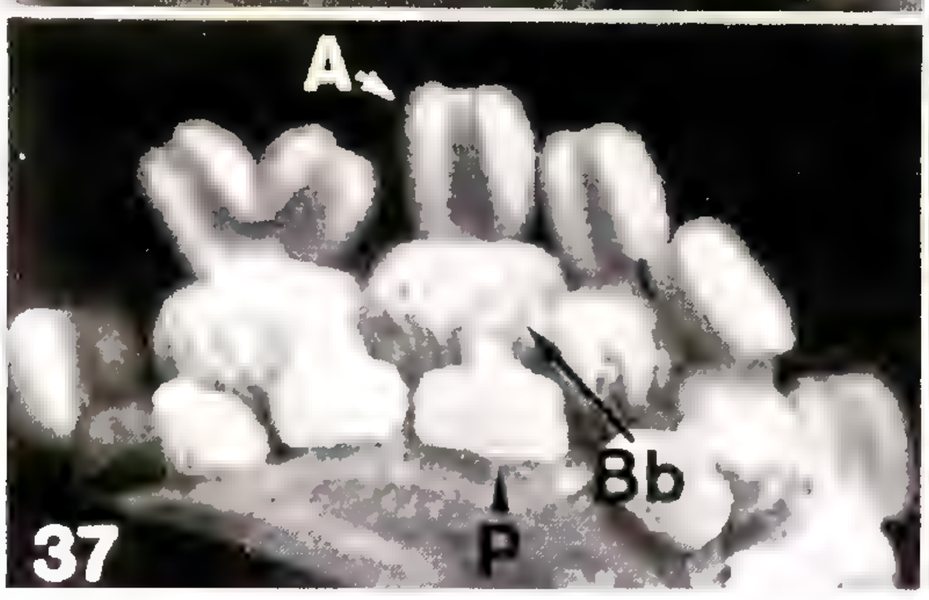
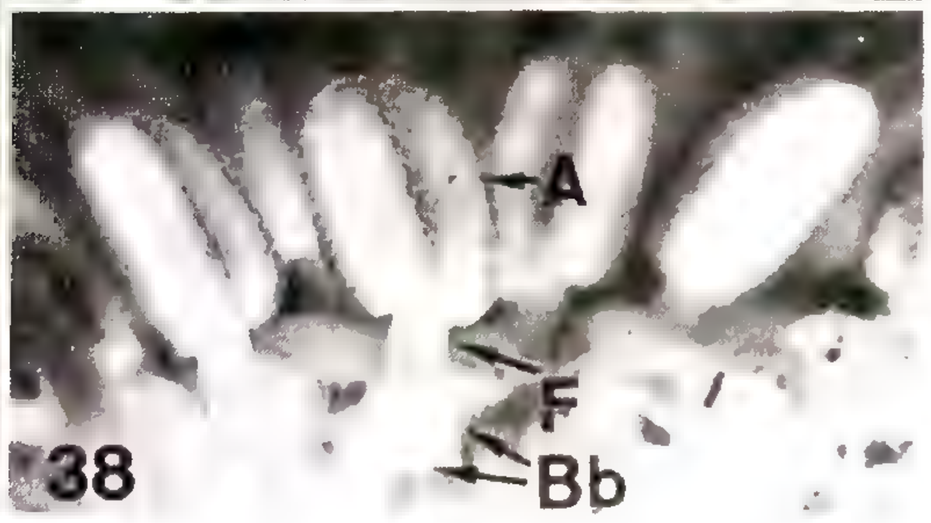
flowers, from below. Flower in FIGURE 29 approximately orbicular; that in FIGURE 30, irregular. P, tepals; Pe, ridge at basal end of pedicel; Sta, stamens; each arrow in FIGURES 26, 28 indicates one arm of V-shaped ridge.









FIGURES 31–38. One whole staminate flower and portions of other staminate flowers from inflorescence illustrated in FIGURES 22–24. 31, 32, largest flower of *Ludovia Bierhorstii*, from above (FIGURE 31) and below (FIGURE 32), both × 7.5. This flower, from basal end of spadix, bears over 100 stamens; its long axis

(5) On staminate flowers of *L. Bierhorstii*, anthers from both marginally and centrally situated stamens tend to be shorter than their counterparts in *L. lancifolia*, respectively, on marginal stamens 0.5–0.7 mm. vs. 0.6–0.9 mm., and on centrally situated stamens 0.7–0.8 mm. vs. 1.4–1.7 mm.

(6) In *L. Bierhorstii* filaments vary from virtually absent to 0.2 mm. long; in *L. lancifolia* filaments are 0.1–0.3 mm. long.

(7) In *L. Bierhorstii* basal bulbs of marginal stamens commonly appear obcordate in side view (FIGURES 35–37), whereas in *L. lancifolia* this is not so (based on Harling's *fig. 89d, f, g*, and on present study of *L. lancifolia*).

Ludovia Bierhorstii differs from *L. integrifolia* as follows:

(1) Maximum lamina width in *L. Bierhorstii* greatly exceeds that in *L. integrifolia* (respectively, 18 cm. vs. 9 cm.), although ranges of lamina length in the two species are roughly comparable. In addition, laminae of the two species differ substantially in shape, those of *L. integrifolia* being elliptical to oblanceolate (however, see later discussion regarding leaf shape).

(2) Maximum numbers of stamens per staminate flower in *L. Bierhorstii* and *L. integrifolia* are, respectively, over 100 vs. 60.

(3) In *L. integrifolia* filaments of all stamens are ca. 0.2 mm. long, in contrast to the condition in *L. Bierhorstii*.

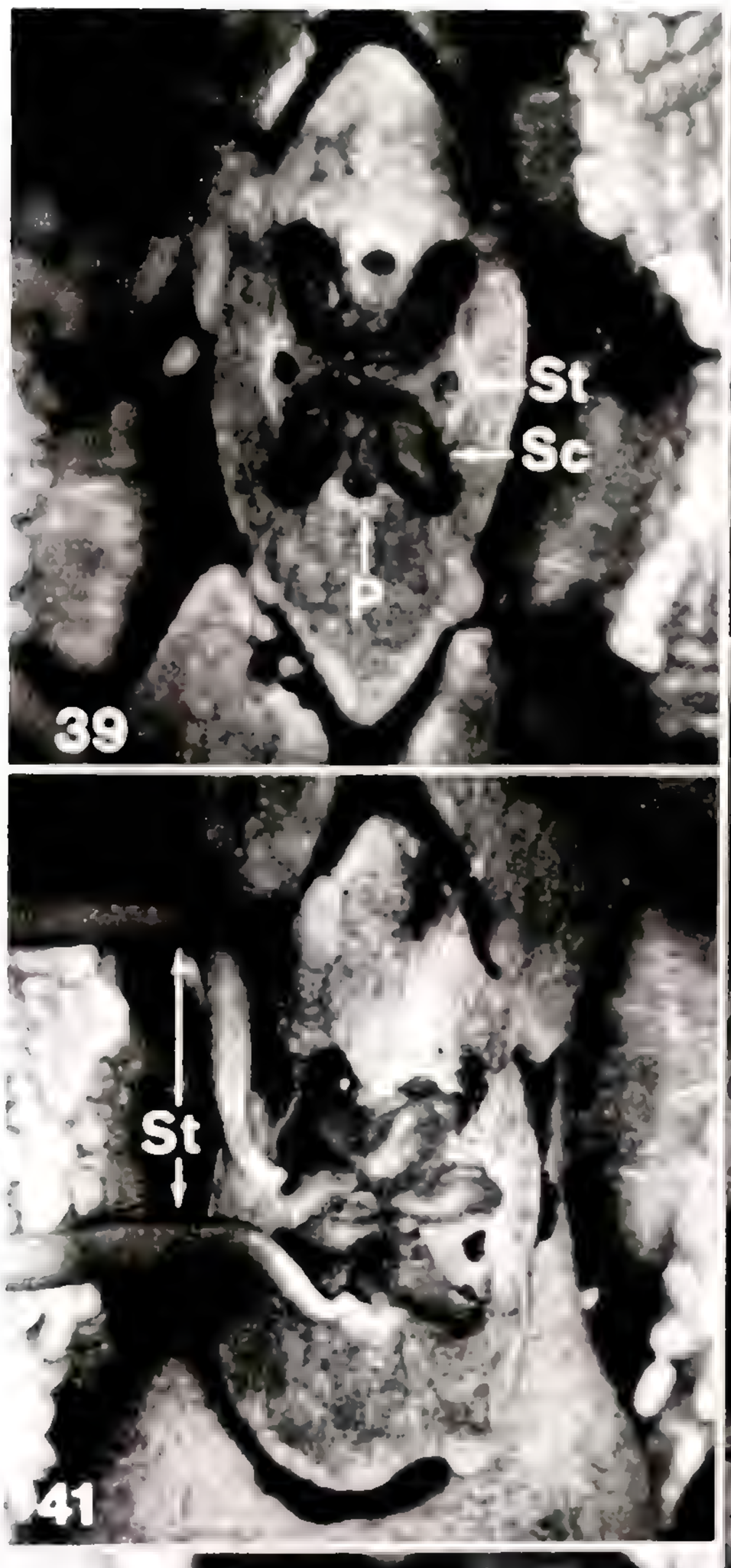
(4) Contrary to the condition in *L. Bierhorstii*, in *L. integrifolia* basal bulbs on marginal stamens are not obcordate in side view (based on Harling's *fig. 91a–c, e, f*, and on present study of *L. integrifolia*).

(5) In *L. integrifolia* stigmas are distinctly laterally compressed, whereas stigmas of *L. Bierhorstii* tend to appear somewhat less compressed and, in addition, substantially more connate to one another (based on Harling's *fig. 91g*, together with present study of both species).

(6) In *L. Bierhorstii* protuberances are abundant and pronounced on that portion of a pistillate flower peripheral to its tepals (FIGURES 39–43, Pr); this is not so in *L. integrifolia* (based on Harling's *fig. 91g* as well as present study of *L. integrifolia*). However, comparable pronounced protuberances have been observed by the author in *L. lancifolia* and, indeed, their presence in *L. lancifolia* is suggested by Harling's *fig. 89h*. Also, in

---

appears curved. Pedicel terminates in slightly arcuate ridge. 33, half of a flower, bisected longitudinally; cut surface, facing viewer, lightly stained, × 10.5. Slight depression at center of flower results from shorter basal bulbs in this region than toward periphery; receptacle essentially flat. 34, staminate flower, from above, × 11.3. All anthers dissected away, exposing basal bulbs; centrally situated basal bulbs appearing much smaller than peripheral ones (dark-staining scar near top of each basal bulb resulting from severance of associated anther). 35–37, abaxial views of stamens situated marginally, × 17, × 15, × 15, respectively. Basal bulb of an apparently single stamen illustrated at left in FIGURE 37 bears two anthers. 38, centrally situated stamens from flower shown in FIGURE 33, illustrated in face view, × 22. On middle stamen note relatively long filament and short basal bulb. A, anther; F, filament; Bb, basal bulb; P, tepal; Pe, ridge at basal end of pedicel.



FIGURES 39–44. Pistillate flowers and portions thereof from region of spadix illustrated in FIGURE 24. 39, 40, tetracarpellate flower, from above (FIGURE 39) and from side (FIGURE 40), × 7.2, × 13, respectively. 41, pistillate flower with five stigmatic crests, from above, × 7.2. Note crest at upper left, branched

L. Bierhorstii protuberances at least partly comprise each tepal (FIGURES 42, 43).

Marginal protuberances of each pistillate flower appear to comprise a discrete group and represent at least positional equivalents of tepals on staminate flowers (e.g., compare FIGURE 42 with FIGURES 26, 28–30, and 32). The marginal protuberances may appear either more or less connate or distinct (e.g., note a few distinct protuberances on the small portion of flower illustrated at bottom of FIGURE 42). As illustrated in FIGURES 42 and 43, protuberances comprising tepals also appear connate to varying extents.

All protuberances might represent modified stamens. If such homology could be demonstrated, our concept of the nature and phylogeny of cyclanthaceous flowers (particularly of their tepals) would be profoundly affected, especially because among cyclanths *Ludovia* appears primitive in various respects (Harling, 1958). Indeed, Garcin (1958) concluded, based on morphological and anatomical studies of various Carludovicoideae (not including *Ludovia*), that each tepal on pistillate flowers of these taxa represents a group of completely sterilized, more or less concrescent staminodes. In light of these possibilities, study of floral development in *Ludovia*, particularly including either *L. Bierhorstii* or *L. lancifolia*, now appears imperative.

The present description of at least vegetative aspects of *Ludovia Bierhorstii* might not accurately reflect morphology of this species in nature, for the following reasons. First, specimens were described from cultivation and they could have developed differently than in nature. Second, because these specimens were genetically homogeneous (a clone), they could not have reflected any genetically based variation which *L. Bierhorstii* as a whole might exhibit. Finally, the material may or may not have possessed an atypical genotype (and hence phenotype) relative to those of most naturally occurring plants of *L. Bierhorstii*. Such uncertainties, together with lack of fertile specimens of *L. Bierhorstii* from nature, preclude definitive conclusions as to whether the described material is conspecific with any or all other previously collected entire-leaved cyclanths from Altaquer and vicinity. Indeed, entire-leaved cyclanths from this region collectively exhibit leaves of diverse morphology and, as discussed below, Harling (1958) included one sterile, entire-leaved specimen from Altaquer in a species of another genus, *Pseudoludovia Andreana*.

Nevertheless, it appears significant that presently described specimens (FIGURES 20, 21), together with all plants I preserved at the collecting locality (including specimens bearing leaves appearing essentially identical to those illustrated by Harling (1958, *plate 86*) under the name *Pseudoludovia Andreana* (FIGURES 45–48)), have the following features in

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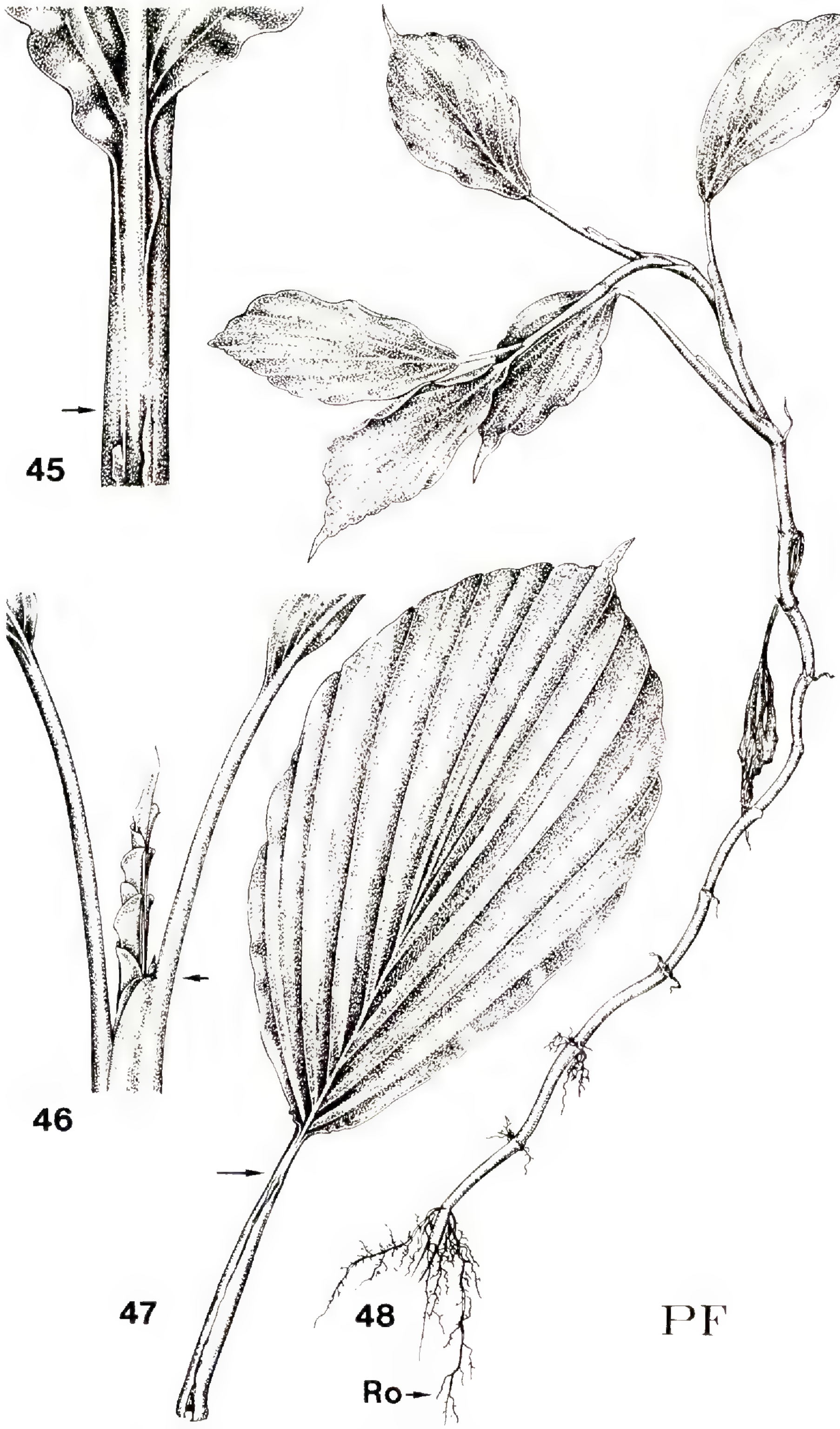
toward periphery of flower. 42, 43, pistillate flowers, from side, both × 18. 44, pistillate flower, from above, × 14. Perianth member at bottom of figure appears three-lobed (each arrow indicating one lobe). P, tepal; Pr, protuberances on portion of pistillate flower situated peripheral to perianth; Sc, stigmatic crest; St, staminode or staminodial scar.



FIGURES 45–48. Material of entire-leaved Cyclanthaceae of uncertain affinity preserved in fluid at Altaquer, Colombia, near type locality of *Ludovia Bierhorstii*. Each arrow not accompanied by symbol indicates boundary between sheath and petiole of leaf. 45, portion of leaf illustrated in FIGURE 47, drawn at higher magnification and in adaxial view, × 1.9. Note winged petiole, each

common. All plants exhibit elongate internodes and distichous phyllotaxy (FIGURES 20, 48). All specimens bear small, varyingly concentrated, red flecks both on stems and sublaminar portions of leaves. The leaves collectively exhibit a virtual continuum of laminar shapes including elliptical, ovate, oblanceolate, obovate, and more or less rhombic. On virtually every leaf, in the sequence listed, lamina, sheath, and petiole (where present) occur in decreasing order of size (FIGURE 49). On the petiole, two adaxial ridges continuous with margins of the lamina occur either along its entire length (where short; FIGURE 45) or on its distal end (where long); such ridges also occur on the specimen in Harling's (1958) *plate 86*. Large leaves each apparently form a cuspidate tip, although this tip is commonly torn away (FIGURES 20, 47, 48).

However, described specimens differ from plants preserved in liquid at the type locality (hereafter called non-described specimens). First, on described plants petioles are typically absent (FIGURES 20, 21, 49) but vary up to 4 mm. long; on non-described specimens petioles are typically but not always present, varying up to 75 mm. long (FIGURES 45–49). However, in being typically non-petiolate (and perhaps in other ways), leaves from described plants may merely exhibit a persistent juvenile feature. Second, on described plants leaves 140 mm. or more long frequently exhibit broadly ovate laminae (FIGURE 20), whereas among non-described specimens leaves in this size range are less commonly ovate. Large, more or less oblanceolate and obovate leaves are common among non-described specimens (FIGURES 47, 48), yet are absent in described material. Third, laminae from described specimens tend to exhibit a higher ratio of width to length (in the investigated size range) than do those from non-described specimens (FIGURE 50).

The discovery that *Ludovia Bierhorstii* represents a new species has cast doubt on the distinctiveness, if not the existence, of *Pseudoludovia Andreana*. This is partly because of the similarity between leaves of *L. Bierhorstii* and those of *P. Andreana* as described by Harling (1958). It would be desirable to collect material of entire-leaved Cyclanthaceae at the type locality of *P. Andreana* in Quindio, Colombia, in order to resolve this problem. If future studies indicate that *P. Andreana* was described on the basis of a mixed collection consisting of sterile material of *Ludovia Bierhorstii* and fertile material of another cyclanth (perhaps a species of *Sphaeradenia*), the epithet "*Andreana*" would more appropriately be assigned to the fertile material than to *L. Bierhorstii*.

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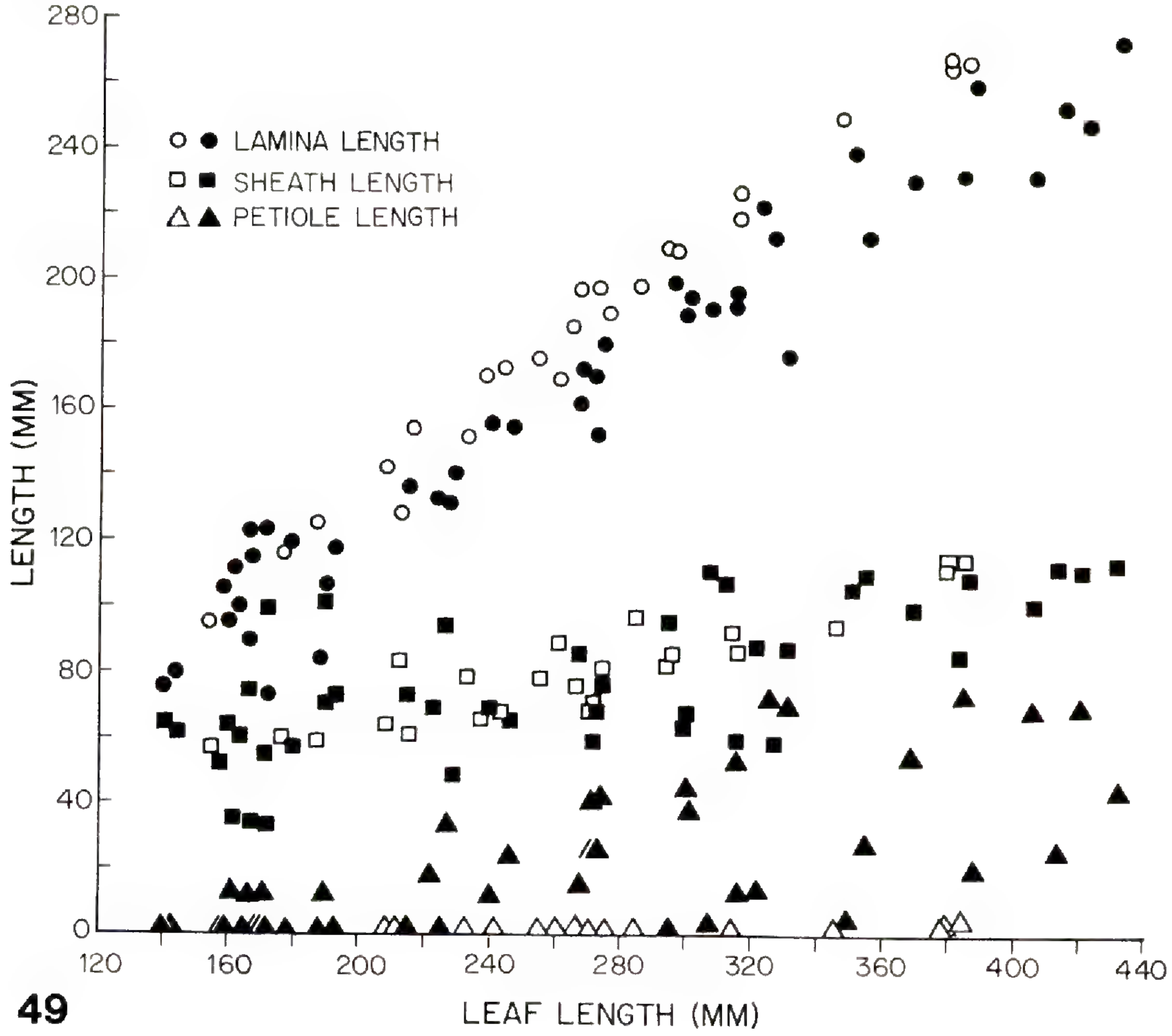
wing continuous with margin of lamina and sheath. 46, portion of shoot tip, × 0.6. Folded, expanding adult leaf at center of illustration enclosed by two unfolded, clearly petiolate, adult leaves. 47, adaxial view of relatively large, obovate, petiolate leaf resembling those illustrated in Harling's (1958) *plate 86* as *Pseudoludovia Andreana*, × 0.3. 48, shoot bearing obovate, petiolate leaves comparable to those illustrated by Harling (1958, *plate 86*), × 0.16. Ro, roots.



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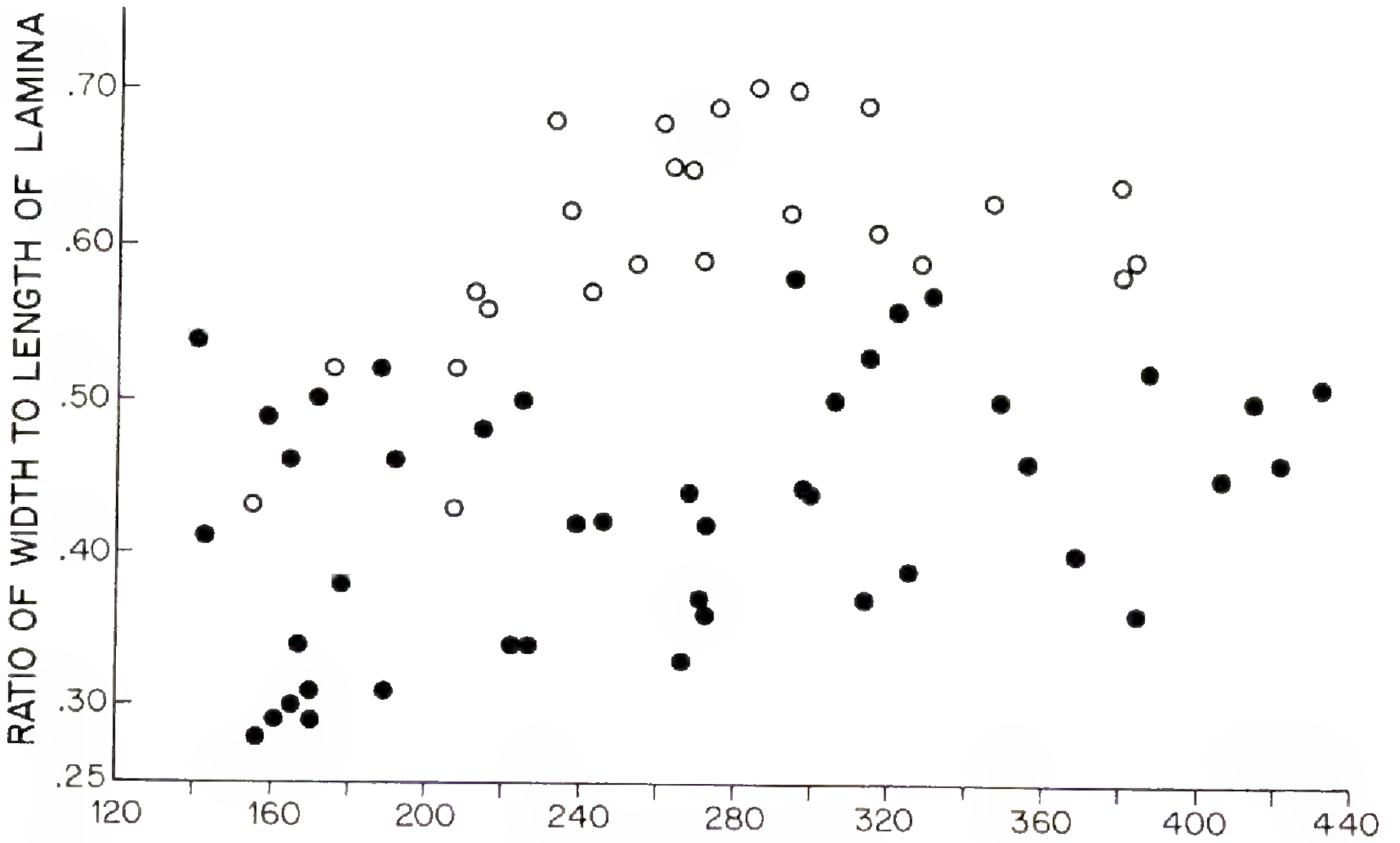

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FIGURES 49, 50. Quantitative data regarding leaves from greenhouse-grown clone of *Ludovia Bierhorstii* and from entire-leaved Cyclanthaceae preserved in liquid at type locality of *L. Bierhorstii*. All leaves from clone were preserved in liquid prior to measurement to assure that data would be comparable. Empty

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Material of *Dicranopygium Harlingii* and *Ludovia Bierhorstii* was collected under a post-doctoral fellowship provided by the Cabot Foundation, Harvard University, and a concomitant appointment at The Fairchild Tropical Garden, Miami, Florida. Funds were also obtained from a National Science Foundation grant (no. GB-31844X, Dr. Philip B. Tomlinson, principal investigator). Additional support for travel came from the Atkins Fund and the Cabot Foundation of Harvard University.

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symbols represent leaves from clone; solid symbols, leaves preserved at type locality. 49, graph indicating relationship between total leaf length and lengths of leaf parts. 50, graph depicting relationship between width and height of lamina.

WOODSON, R. E., JR., & R. W. SCHERY. 1942. Contributions toward a flora of Panama. VI. Collections chiefly by H. von Wedel in Bocas del Toro. Ann. Missouri Bot. Gard. **29**: 317–379. *pls. 30–34.*

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COVER: The stylized representation of fruits of various Leguminosae, forming the design of our new cover for Volume 59, is based on material from plants growing in the Arnold Arboretum of Harvard University. The design was planned and executed by Karen S. Velmure, who has also drawn several of the preceding covers as well as various devices used in the *Journal of the Arnold Arboretum* and on the offprint covers.

The three subfamilies of the Leguminosae are represented by the fruits shown in the design. The genera are, top row (left to right), *Albizia* (Mimosoideae), *Gleditsia* (Caesalpinioideae), *Caragana* (Faboideae), *Gymnocladus* (Caesalpinioideae), and lower row, right, *Colutea* (Faboideae).

The family Leguminosae, the second most important family of flowering plants, is to be the subject of an International Legume Conference at the Royal Botanic Gardens, Kew, Richmond, Surrey, England, in July, 1978. This cover is our salute to the complete success of that Conference.

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FORM OF THE PERFORATION PLATES IN THE WIDE VESSELS OF METAXYLEM IN PALMS

LARRY H. KLOTZ

THIS ARTICLE SUMMARIZES the results of a survey (Klotz, 1977) of the form of the perforation plates in the wide vessels of the metaxylem in the family Arecaceae, the palms. The objective is to compare and contrast this feature in petiole, stem, and root among the taxonomic and ecological groups of palms.

The form of tracheary elements is an important character in plant systematics (Carlquist, 1975), and its significance in plant physiology and autecology is recognized in regard to the efficiency and safety of water conduction (Zimmermann, 1978). The present work is complementary to the series of intensive studies that Cheadle has produced on tracheary elements within various other families of monocotyledons (e.g., Cheadle & Kosakai, 1975). Before the present study was undertaken, the palms were among the large families of monocotyledons that remained to be examined in detail, although Cheadle (1942), Mahabalé (1959), and Tomlinson (1961, 1965, 1966, 1969) had published data on perforation plates in various species of palms.

A large family of about 2800 species in over 200 genera (Moore, 1973), the palms deserve thorough anatomical investigation for several reasons. They are important economically for various natural products and for ornament. Unfortunately, some of the cultivated species are currently being ravaged by lethal diseases (Fisher, 1975). Palms compose a significant part of the vegetation in many kinds of tropical and subtropical ecosystems (Moore, 1973). Finally, the palms are of theoretical importance in plant systematics for their combination of primitive and advanced features (Moore & Uhl, 1973), and in plant anatomy and physiology for their large "woody" habit and their complicated vascular structure (Tomlinson & Zimmermann, 1967).

MATERIALS AND METHODS

Tracheary elements were examined in the petiole or the rachis of 209 species, the stem of 169 species, and the root of 136 species of palms. All

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15 of the major taxonomic groups in the family (Moore, 1973) were represented. Specimens of some genera were difficult or impossible to obtain, especially stems of large, single-stemmed palms. All three vegetative organs were sampled in at least one species of every genus for which material was available except those species within the large arecoid major group. In this group, all but one of the generic alliances were sampled; and in the alliances with more than one genus, species from two or more genera were examined, depending on the size of the alliance. Within two of the larger genera, *Bactris* and *Chamaedorea*, species were selected from each of the principal subgenera or sections.

Specimens were obtained from natural populations in native habitats or from cultivated collections in botanical gardens, and where possible were vouchered with an herbarium specimen. Collection data for the specimens and the authors of the species are available (Klotz, 1977).[1]

The specimens were taken from plants with mature leaf morphology and stem diameter. The segments of first-order roots preferred were fairly straight and had few or no branches. Most of the stems were sampled within the central one-third of the stem diameter. The position of the sample along the length of the stem was usually not known, but the middle of the length was selected where possible. Petioles were sampled in the central (i.e., interior) part, preferably at midlength. In species lacking pronounced petioles, a segment of the proximal part of the rachis, between insertions of the pinnae, was examined.

Specimens fixed in FAA (Johansen, 1940) and dried herbarium specimens were used. The latter were softened by boiling them in water. Each specimen was sectioned transversely with razor blades or a sliding microtome. The remaining portion was cut into slivers that were macerated in Jeffrey's solution (Johansen, 1940) and stained with Delafield's hematoxylin. Additional details of the procedure are given by Klotz (1977).

One piece from one organ of an individual usually constituted the sample. In a few species, similar samples from two different collections were examined. Using the same piece for both transverse sections and maceration allowed correlation of cells in the maceration with the position of comparable cells in the corresponding transverse section. For almost all specimens at least 10 intact wide vessel elements of metaxylem were studied. The characteristics of the perforation plates are thus based on 20 or more perforation plates from 10 or more wide vessel elements. Successive elements of one vessel as well as vessel elements from several different vascular bundles were examined. Narrow tracheary elements were also obtained.

[1] Specimens from stems of three species of borassoid palms were examined after completion of the thesis (Klotz, 1977) but are included in the tabulations of this article: *Bismarckia nobilis* — Subtropical Horticultural Research Station, U. S. Dept. Agriculture, Miami, Fla., P. I. 106–556–7514; *Borassus aethiopum*; and *Hyphaene guineensis*. All three specimens were collected by P. B. Tomlinson. The latter two had been examined by him previously and listed with author citations and collection data (Tomlinson, 1961).

DEFINITIONS AND CATEGORIES

TRACHEIDS AND VESSEL ELEMENTS. In this study vessel elements are distinguished from tracheids on the basis of the shape of the cell and the configuration of the secondary wall. More specifically, vessel elements have end walls in which the apertures between the bars of secondary wall are wider than the comparable apertures on the lateral walls — i.e., the intervessel pits. Such end walls are either true perforation plates or, at least, distinctive contact areas between successive tracheary elements.

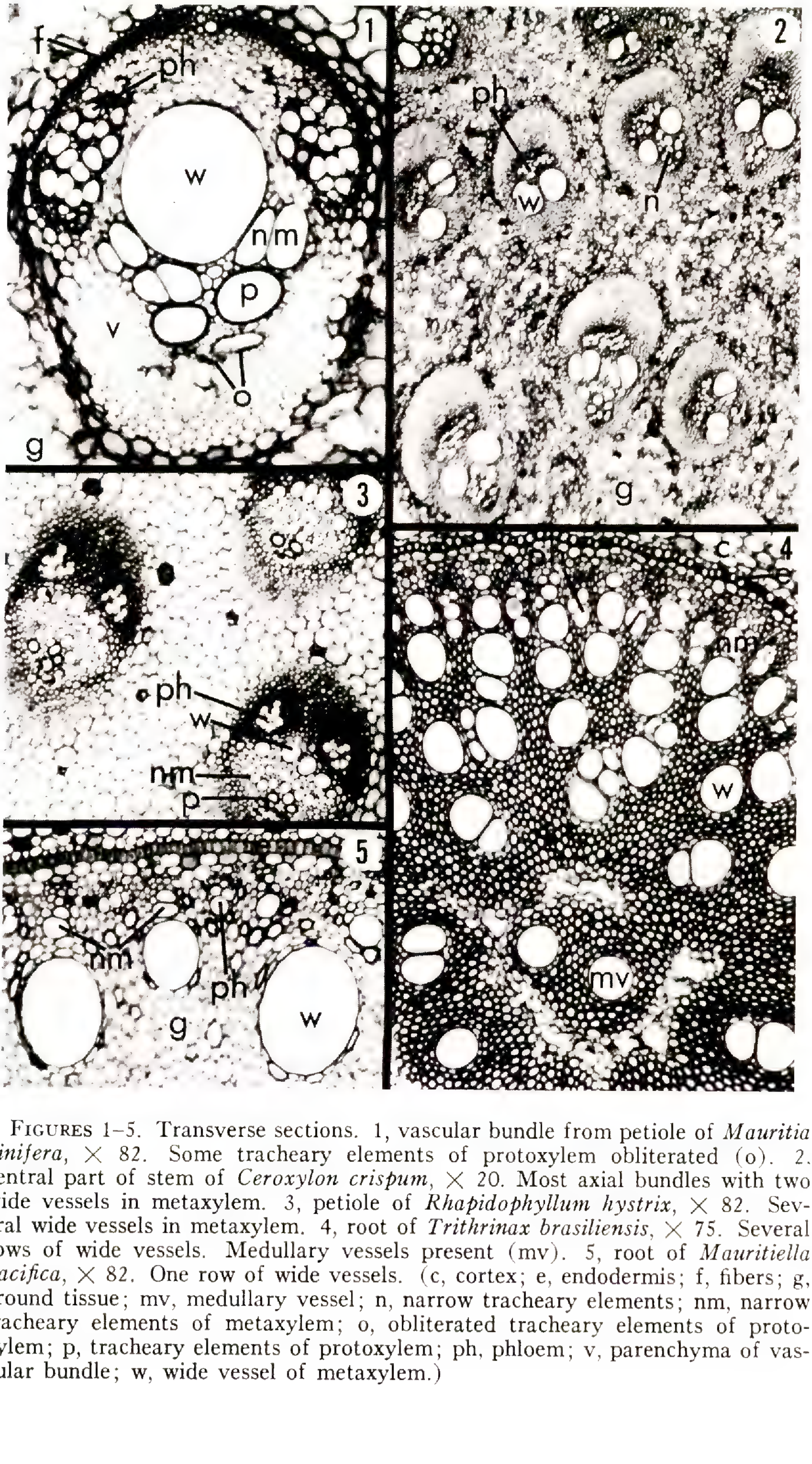
By definition, tracheids are imperforate cells with only pit-pairs on their contiguous walls, whereas vessel elements are perforate in certain areas of contiguity with other vessel elements (Esau, 1965). However, this distinction is often difficult to make because the difference between tracheid and vessel element or between pit and perforation can be a matter of degree. Distinct pit membranes across the apertures of the end walls of the wide tracheary elements were usually not observed in longitudinal sections with light microscopy, but it is possible that embedding in celloidin or some other plastic might have yielded positive results in more specimens. Scanning electronmicroscopy (SEM) reveals that variable amounts of hydrolyzed primary wall (i.e., pit membrane) can remain across perforation apertures in palms (Klotz, 1977; Parthasarathy & Klotz, 1976).

PRIMITIVE AND ADVANCED. The terms "primitive" and "advanced" are used to express the degree of resemblance of vessel elements to tracheids. Thus, primitive vessel elements have long, extremely oblique or very oblique end walls in which the perforation plates have many bars that are closely spaced, and advanced vessel elements have slightly oblique to transverse end walls on which the bars are few or absent (Cheadle, 1943a).

NARROW AND WIDE TRACHEARY ELEMENTS. In vascular bundles of the shoot, one (FIGURE 1), two (FIGURE 2), or more than two (FIGURE 3) of the tracheary elements of the metaxylem are markedly wider than the other tracheary elements. In roots, the tracheary elements toward the center of the root are usually wider than those nearer the endodermis (FIGURES 4, 5). The widest tracheary elements in the vascular bundles of the shoot or in the stele of the root are termed "wide"; the remainder are termed "narrow."

END WALL SLOPE. Cheadle's (1943a) classification of end wall slopes is employed with the addition of the category "extremely oblique" for especially long end walls:

e (extremely oblique)	end wall >10 times as long as cell width
v (very oblique)	end wall >5 to ≤ 10 times as long as cell width
o (oblique)	end wall >2 to ≤ 5 times as long as cell width
s (slightly oblique)	end wall >1 to ≤ 2 times as long as cell width
t (transverse)	end wall perpendicular to lateral wall



FIGURES 1–5. Transverse sections. 1, vascular bundle from petiole of *Mauritia vinifera*, × 82. Some tracheary elements of protoxylem obliterated (o). 2. central part of stem of *Ceroxylon crispum*, × 20. Most axial bundles with two wide vessels in metaxylem. 3, petiole of *Rhapidophyllum hystrix*, × 82. Several wide vessels in metaxylem. 4, root of *Trithrinax brasiliensis*, × 75. Several rows of wide vessels. Medullary vessels present (mv). 5, root of *Mauritiella pacifica*, × 82. One row of wide vessels. (c, cortex; e, endodermis; f, fibers; g, ground tissue; mv, medullary vessel; n, narrow tracheary elements; nm, narrow tracheary elements of metaxylem; o, obliterated tracheary elements of protoxylem; p, tracheary elements of protoxylem; ph, phloem; v, parenchyma of vascular bundle; w, wide vessel of metaxylem.)

The distinction between transverse and slightly oblique is somewhat subjective but is adhered to rather strictly. In many samples, especially those from roots, end walls range from apparently perpendicular to the length of the cell to only a few (≤ 15) degrees from the perpendicular — i.e., they are very slightly oblique.

The overall or net slope of curved end walls was estimated. Ligules (FIGURES 36–38) were not included in determining slope.

Two methods were devised to summarize the data. First, proportional frequencies were determined for the five categories of slope for each organ in each major group. Each species was given equal weight, even if more vessel elements had been obtained from some specimens than from others. The proportional frequencies are presented as histograms (FIGURE 41). Second, "slope indexes" (TABLE 1) were calculated for each organ according to the formula:

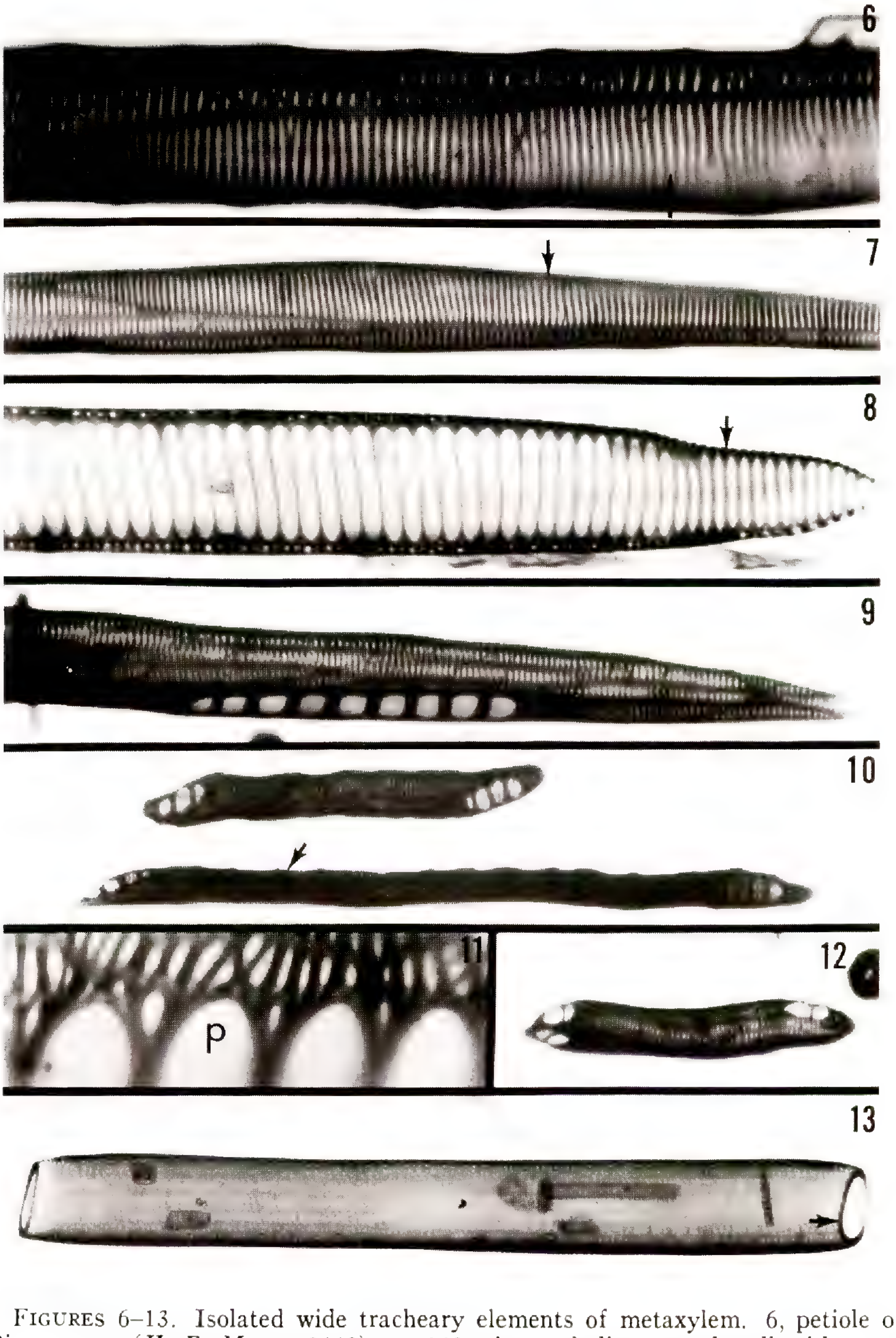
slope index $\times$ 100 = 0 (% tracheids) + 1 (% extremely oblique end walls) + 2 (% very oblique end walls) + 3 (% oblique end walls) + 4 (% slightly oblique end walls) + 5 (% transverse end walls)

Average slope indexes were calculated for the organs in each of the major groups, and "total slope indexes" were calculated by adding the average slope indexes for the three organs. In this way, a single numerical value was obtained to summarize the average slope of the end walls in each of the major groups. In TABLE 1, the total slope indexes of the major groups are listed in order of increasing value (or decreasing obliqueness).

In the iriarteoid major group, the average slope index for the aerial roots is lower than that for the subterranean roots. Since the two kinds of roots are not from the same species, total slope indexes for the iriarteoid palms are calculated both ways (TABLE 1).

"SPECIALIZATION VALUES." "Specialization values" are assigned to the samples of perforation plates of the wide vessel elements of metaxylem according to the following system, which includes categories for describing the relative spacing of bars of secondary wall in multiple perforation plates. This system differs from the one invented by Cheadle for other groups of monocotyledons (e.g., Cheadle & Kosakai, 1975) in order to express the data for palms in more detail.

0 — tracheids only — definite vessels not observed
1 — multiple perforation plates with "pitlike" perforations that span ≤ 1 vessel–parenchyma pit on the adjacent lateral wall (FIGURES 6, 7)
2 — multiple perforation plates with "narrow" perforations that span > 1 to ≤ 2 vessel–parenchyma pits (FIGURE 8)
3 — multiple perforation plates with "medium-size" perforations that span > 2 to ≤ 5 vessel–parenchyma pits (FIGURES 9, 11, 23)
4 — multiple perforation plates with "wide" perforations that span > 5 vessel–parenchyma pits (FIGURE 15), or with ≤ 3 bars



FIGURES 6–13. Isolated wide tracheary elements of metaxylem. 6, petiole of *Pinanga* sp. (*H. E. Moore 9112*), × 240. Arrow indicates end wall with apertures more closely spaced than pits of adjacent lateral wall. 7, stem of *Wendlandiella polyclada*, × 240. Arrow indicates end wall with apertures about as closely spaced as pits of adjacent lateral wall. 8, root of *Physokentia rosea*, × 240. End wall with each perforation spanning about two pits of adjacent lateral wall. Arrow indicates narrower apertures, possibly intervessel pits, in distal part of end wall. 9, stem of *Lepidocaryum gracile*, × 140. End wall in which perforations, separated by wide bars, each span about five pits of adjacent

TABLE 1. **Total average slope indexes for the major groups.**

MAJOR GROUP		SLOPE INDEX
XI.	Pododoccoid	7.3
IX.	Chamaedoreoid: smaller species	7.4
IX.	Chamaedoreoid: total	8.1
XV.	Phytelephantoid *	8.2
V.	Nypoid	8.6
XIV.	Geonomoid	8.9
VIII.	Ceroxyloid	9.1
X.	Iriarteoid: including aerial roots	9.1
XII.	Arecoid	9.3
X.	Iriarteoid: including subterranean roots	9.4
IX.	Chamaedoreoid: larger species	10.0
II.	Phoenicoid	10.1
IV.	Lepidocaryoid: non-lianas	10.9
VII.	Pseudophoenicoid	11.2
I.	Coryphoid	11.2
XIII.	Cocosoid	11.2
III.	Borassoid	11.4
VI.	Caryotoid	11.5
V.	Lepidocaryoid: total	12.0
IV.	Lepidocaryoid: lianas	12.6

* Including *Ammandra*, with only tracheids in the stem.

5 — mixture of multiple perforation plates (as in #4) and simple perforation plates
6 — simple perforation plates only (FIGURE 13)

Samples that span two adjacent categories are assigned values of "½"; for example, "3½" expresses samples of multiple perforation plates with bars of "medium" to "wide" spacing, and "5½" expresses samples in which the end walls bear one or no bars. Mixed samples that span a wider range of categories are designated with "a":

2½a — perforation plates in sample range from 1 to 4
3a — from 2 to 4
3½a — from 2 to 5 (or 6)
4a — from 3 to 5 (or 6)

lateral wall. 10, stem of *Chamaerops humilis*, × 100. Vessel elements with slightly crooked or scalloped (arrow) lateral walls. Perforation plates have few bars. 11, stem of *Euterpe cuatrecasana*, × 750. Detail of vessel element with each perforation (p) spanning about five pits of adjacent lateral wall. 12, stem of *Rhapidophyllum hystrix*, × 120. Vessel element with one bar in each of three perforation plates. 13, stem of *Calamus muelleri*, × 100. Vessel element with simple perforation plates. Arrow indicates broad flange of secondary wall around perforation.

A similar procedure was applied to Cheadle's system of specialization values (Cheadle, 1955), which considers only the relative abundance of multiple perforation plates versus that of simple perforation plates:

0 — tracheids only
1 — multiple perforation plates only
2 — ≤1/3 simple perforation plates
3 — >1/3 simple to ≤2/3 simple
4 — >2/3 simple
} mixed multiple and simple perforation plates
5 — simple perforation plates only

The values refer only to the wide tracheary elements of the metaxylem. For values 2 through 4, Cheadle does not specify exact percentages but lets 2 stand for "mostly scalariform"; 3, for "about equal scalariform and simple"; and 4, for "mostly simple" (Cheadle & Kosakai, 1975).

Within the taxonomic groups of palms, the means of the specialization values were calculated for each organ and were plotted as points (FIGURES 42, 43). A vertical line through a point indicates the range of specialization

TABLE 2. **Total average specialization values for the major groups.**

AUTHOR'S SYSTEM		CHEADLE'S SYSTEM	
Chamaedoreoid: small species	5.1	Nypoid	3.0
		Chamaedoreoid: small species	3.0
Iriarteoid: aerial roots	6.2		
Chamaedoreoid: total	6.3	Chamaedoreoid: total	3.7
Podococcoid	6.5	Iriarteoid: aerial roots	3.8
Iriarteoid: subterranean roots	7.1		
		Iriarteoid: subterranean roots	5.0
Nypoid	8.0	Chamaedoreoid: large species	5.5
Ceroxyloid	8.3	Arecoid	5.8
Geonomoid	8.6	Pseudophoenicoid	6.0
Arecoid	9.0	Podococcoid	6.0
Phytelephantoid *	9.0	Geonomoid	6.0
		Ceroxyloid	6.5
Chamaedoreoid: large species	9.7	Phytelephantoid *	6.7
		Caryotoid	7.6
Pseudophoenicoid	10.5	Cocosoid	7.8
		Phoenicoid	8.0
Coryphoid	11.9	Lepidocaryoid: non-lianas	8.6
Caryotoid	11.9	Coryphoid	8.8
Phoenicoid	12.0		
Cocosoid	12.1		
		Borassoid	10.0
Lepidocaryoid: non-lianas	13.2		
Borassoid	13.4	Lepidocaryoid: total	10.8
Lepidocaryoid: total	14.5	Lepidocaryoid: lianas	11.9
Lepidocaryoid: lianas	15.0		

* Including *Ammandra*, with only tracheids in the stem.

values for the organ in the group. The three points on each chart (for petiole, stem, and root) are connected by lines merely to make the patterns easier to perceive.

The specialization values were further summarized by adding the averaged values for petiole, stem, and root in the major groups of palms (TABLE 2). In the iriarteoid major group, the average value for the aerial roots is lower than that for the subterranean roots. Since the two kinds of roots are not from the same species, the total average specialization values for the iriarteoid palms are calculated both ways.

OBSERVATIONS

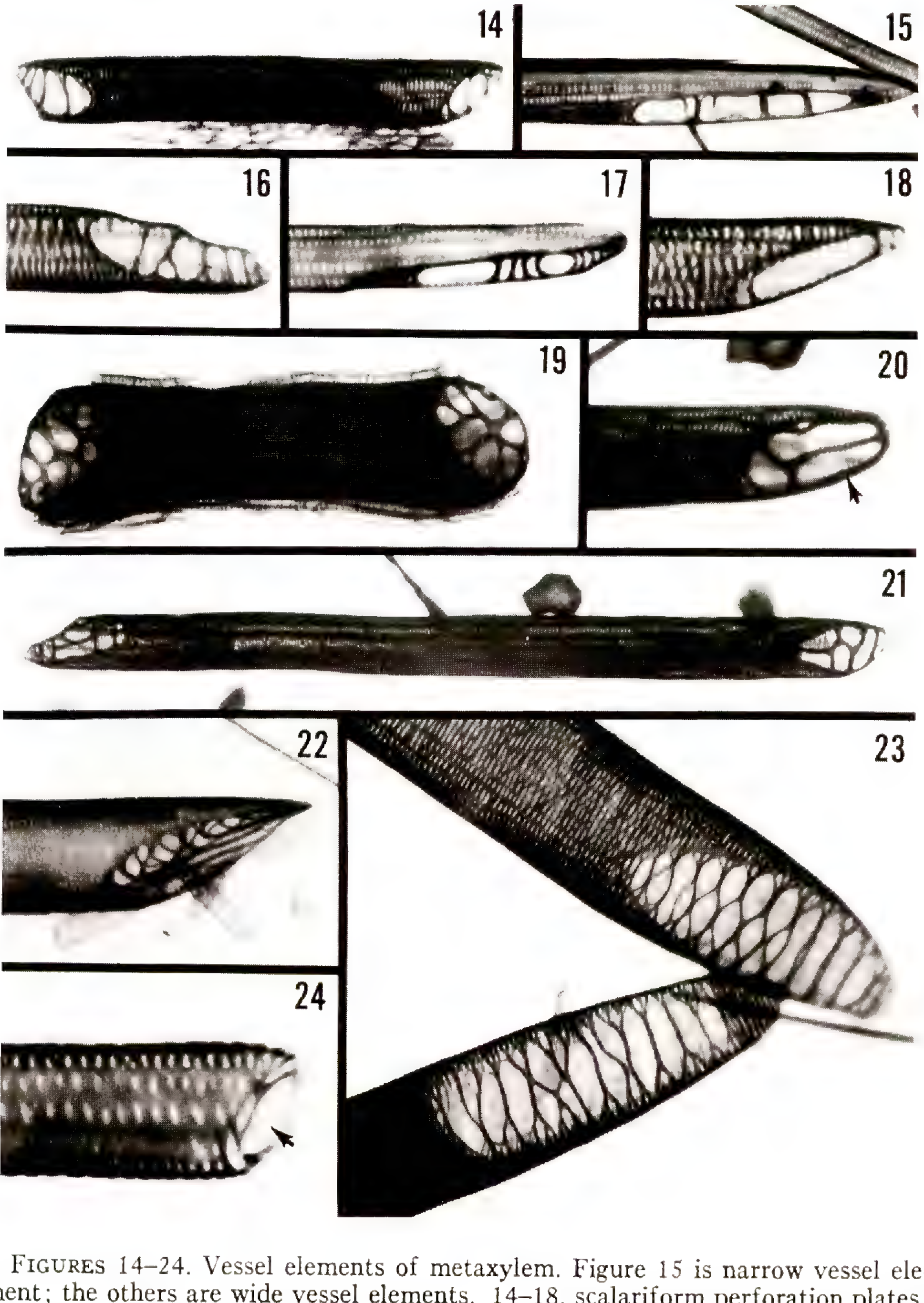
KINDS OF PERFORATION PLATES. The wide tracheary elements of the metaxylem are vessel elements, except possibly in the rhizomatous stem of the phytelephantoid palm *Ammandra decasperma*. Multiple and/or simple perforation plates occur in the wide vessels.[2] Most of the multiple perforation plates are basically scalariform. The most tracheid-like variety contains many bars on steeply sloping end walls in which the perforations are less widely spaced than the adjacent vessel–parenchyma pits of the lateral walls, but more widely spaced than the intervessel pits (FIGURE 6). This primitive variety grades into perforations that are about as closely spaced as the adjacent vessel–parenchyma pits of the lateral walls (FIGURE 7). In successive forms there is a gradation toward fewer, more widely spaced bars (FIGURES 8–11, 14–18); to only one bar (FIGURE 12); and finally, in the advanced extreme of the series, to no bars (FIGURE 13). Paralleling this gradation is a general decrease in the slope of the end wall.

Where perforations are narrow, the bars of the perforation plates are usually spaced evenly; but with wider spacing of bars, the bars tend increasingly toward irregular spacing (FIGURES 14–18). Bars of perforation plates frequently branch and anastomose to varying degrees (FIGURES 23, 28, 29) and rarely end blindly (FIGURES 28, 31).

The gyres of secondary wall that compose the bars of a perforation plate sometimes appear incompletely "fused" to varying degrees (FIGURE 30). The apertures between such "unfused" gyres are often no wider than the pits of the lateral walls, but sometimes they approach the width of the major perforations.

Reticulate perforation plates are the other basic type of multiple perforation plate (FIGURES 19–22, 24). An extreme variation of this type consists of only one bar, which is oriented longitudinally rather than transversely in the perforation plate. In another distinctive variation, a large, central perforation is surrounded by smaller apertures that are larger than the pits of the lateral walls (FIGURE 24). Reticulate perforation plates intergrade with scalariform perforation plates through a great diversity of forms. These intermediate, "scalariform-reticulate" configurations range

[2] The terminology for perforation plates is from Esau (1965).



FIGURES 14–24. Vessel elements of metaxylem. Figure 15 is narrow vessel element; the others are wide vessel elements. 14–18, scalariform perforation plates: 14, stem of *Pseudophoenix sargentii*, × 82, few bars, unevenly spaced; 15, root of *Calamus perakensis*, × 260, few bars, unevenly spaced and unequal in width; 16, root of *Aiphanes* sp., × 140, few bars, unevenly spaced; 17, root of *Chelyocarpus dianeurus*, × 140, bars very unevenly spaced; 18, root of *Physokentia rosea*, × 140, one large, central perforation. 19–22, reticulate perforation plates: 19, stem of *Sclerosperma mannii*, × 88; 20, stem of *Lepidocaryum gracile*, × 100 (arrow indicates flange of secondary wall surrounding most of perforation plate); 21, stem of *Lepidocaryum gracile*, × 66; 22, petiole of *Daemonorops grandis*, × 300. 23, scalariform-reticulate perforation plates: stem of *Clinostigma savaiiense*, × 75, branching and anastomosing of bars rather regular (upper ves-

from highly regular, lattice-like arrangements of many bars spaced rather closely (FIGURES 25, 26) to arrangements in which the spacing of the bars is more sparse and/or irregular (FIGURES 23, 27, 29, 31).

Perforation plates also vary in other ways. Bars of the end wall may be thicker (FIGURE 9), similar in thickness (FIGURE 7), or thinner (FIGURE 8) than the gyres of the lateral wall. The widths of the bars may be uniform (FIGURE 8) or variable (FIGURE 15) throughout the length of a perforation plate. A flange or rim of secondary wall frames many simple perforation plates (FIGURE 13) and some multiple perforation plates, especially those with few or widely spaced bars (FIGURES 20, 31). Perforation plates may extend the entire length (FIGURE 26) or only part of the length of the end wall. In the latter category, there is a gradual or abrupt transition from perforations to intervessel pits at the proximal end of the perforation plate (FIGURES 33, 34), at the distal end (FIGURES 8, 9), or at both ends. This character is often highly variable within a sample. End walls also occur in which the perforations do not extend to the lateral margins of the end wall (FIGURE 35). Vessel elements with intervessel pitting on the end wall distal to the perforation plate intergrade with vessel elements in which an extension of the cell continues distally beyond the end wall but is not part of it. Such extensions, called ligules, vary in shape and relative size (FIGURES 36–38). End walls are usually quite straight, but occasionally they are curved or even "saddle-shaped" (FIGURE 39). Perforation plates rarely occur on the lateral walls.

END WALL SLOPE. The histograms of proportional frequencies (FIGURE 41) indicate that slopes of end walls are generally greatest in the petiole, intermediate in the stem, and lowest in the root. The only significant exception to this trend is the phytelephantoid *Ammandra decasperma*, in which clearly discernible vessels were not found in the stem.

Some of the major groups are rather heterogeneous in slopes of end walls (TABLE 1, FIGURE 41). End walls tend to be less oblique in the larger chamaedoreoid species than in the smaller chamaedoreoid species. End walls also tend to be less oblique in the lepidocaryoid lianas than in the other lepidocaryoid palms.

"SPECIALIZATION VALUES." The diagrams of average specialization values of perforation plates in the major groups of palms indicate that bars in the perforation plates of the wide tracheary elements of the metaxylem are generally most closely spaced in the petiole, intermediate in the stem, and most widely spaced (or fewest) in the root (FIGURE 42). The only significant exception to this tendency is *Ammandra decasperma*, in which clearly discernible vessels were not observed in the stem. The diagrams according to Cheadle's system (FIGURE 43) show that multiple perforation plates are most frequent in petioles, intermediate in stems, and least frequent in roots.

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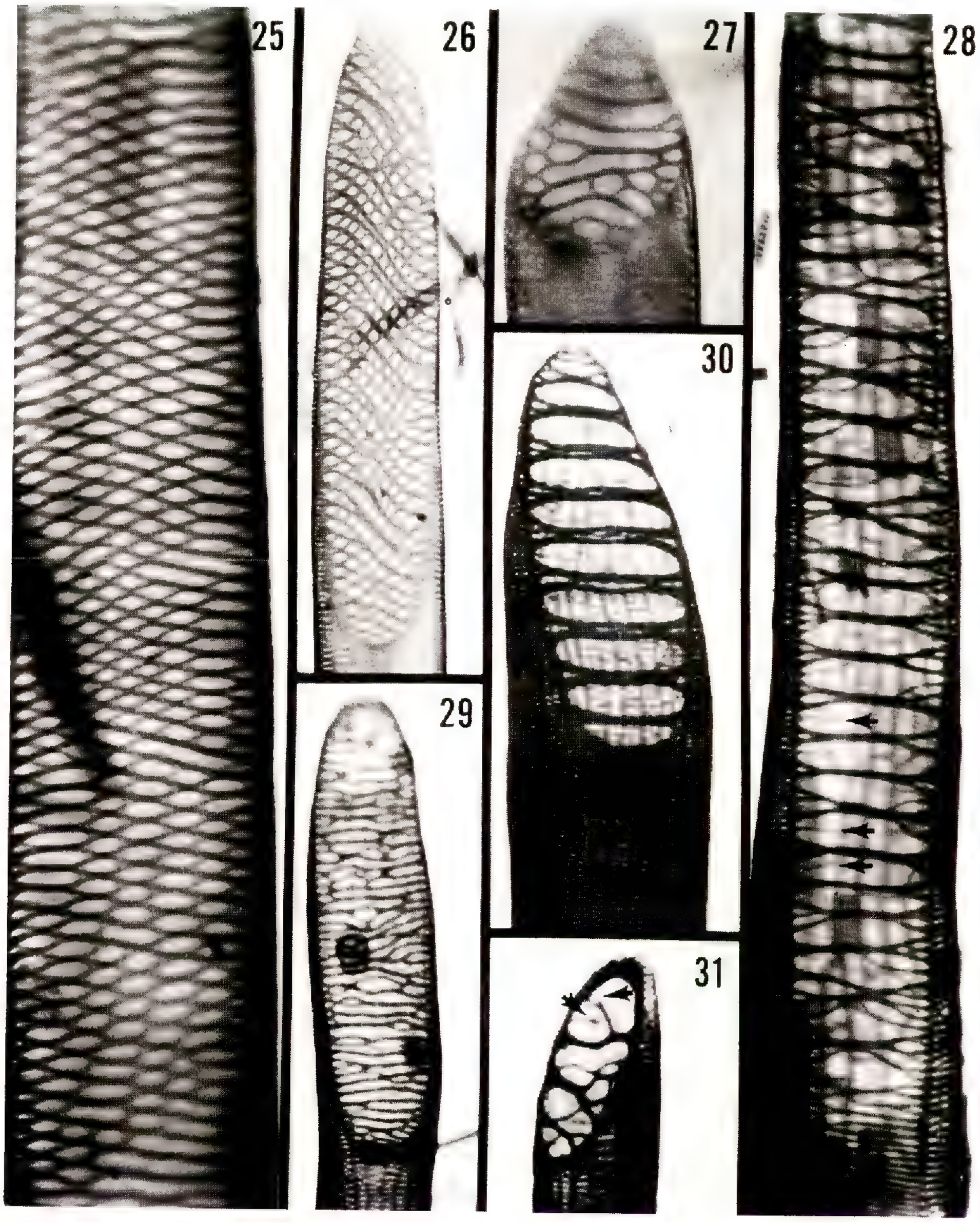
sel element) or irregular (lower vessel element). 24, reticulate perforation plate: root of *Reinhardtia simplex*, × 340, single large perforation (arrow) surrounded by smaller perforations.



FIGURES 25–31. Wide vessel elements of metaxylem. 25–27, scalariform-reticulate perforation plates: 25, petiole of *Polyandrococos caudescens*, × 240, bars connected by numerous crossbars, both sets of bars very evenly spaced; 26, petiole of *Daemonorops grandis*, × 110, two scalariform configurations appear to be superposed at right angles to form screenlike configuration; 27, petiole of *Arenga undulatifolia*, × 180. 28, scalariform perforation plate: stem of *Clinostigma savaiiense*, × 88, bars much branched, especially toward sides of perforation plate; some narrow bars end blindly (arrows). 29, scalariform-reticulate perforation plate: rachis of *Eremospatha* sp., × 100. 30, scalariform perforation plate: stem of *Mauritia vinifera*, × 65, gyres of secondary wall that form bars between the large perforations appear incompletely "fused" to varying degrees. 31, scalariform-reticulate perforation plate: petiole of *Calamus siphonospathus*, × 140, some narrower bars ending blindly (arrows) and peripheral flange of secondary wall.

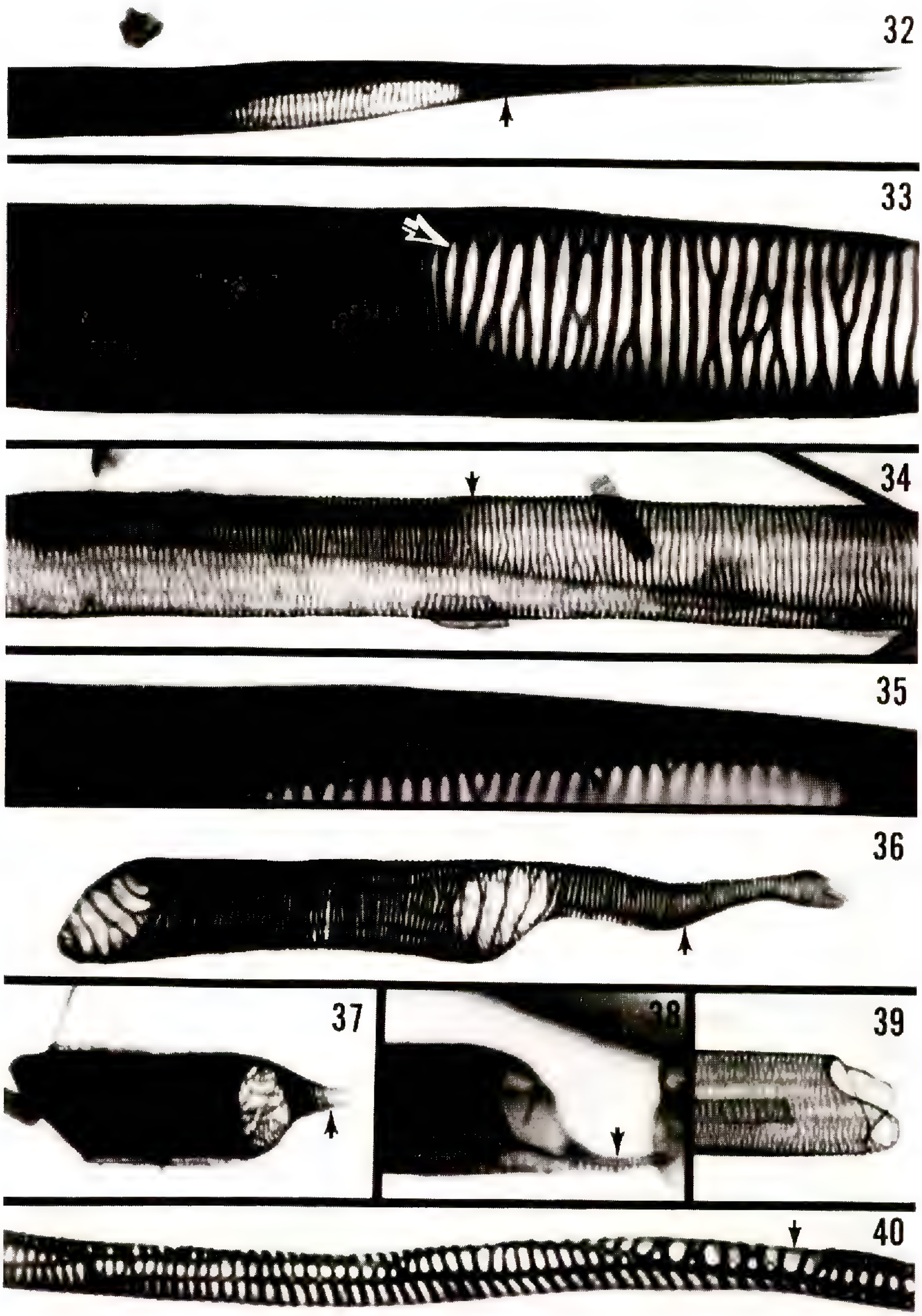
The positions of the major groups in TABLE 2 are generally similar in the two schemes. The major groups are clustered along the continuum of numerical values. At the lower end are the chamaedoreoid (especially the small species) and iriarteoid palms. Above them is a cluster that includes the ceroxyloid, arecoid, geonomoid, and phytelephantoid palms. The larger chamaedoreoid species and *Pseudophoenix* are also in or near this cluster. *Nypa* and *Podococcus* belong to one of the two lower clusters of groups in both schemes. The next cluster in the series includes the coryphoid, phoenicoid, caryotoid, and cocosoid palms. The nonscandent lepidocaryoid palms also belong in or near this cluster in both schemes. Finally, at the higher end of the spectrum are the borassoid palms and the lepidocaryoid lianas.

The spacing of bars in perforation plates (FIGURE 42) and the distribution of multiple and simple perforation plates (FIGURE 43) show trends that parallel those shown by the slopes of end walls (FIGURE 40). According to all three criteria, perforation plates are most primitive in the petiole, intermediate (or else similar to either petiole or root) in the stem, and most advanced in the root. This generalization applies to the individual species and to the average values in the major groups. Among the major groups of palms (TABLES 1, 2) the average values of the three criteria indicate that the chamaedoreoid palms (especially the smaller species) are among the most primitive groups. *Nypa* is also fairly primitive, as are the ceroxyloid, iriarteoid, arecoid, and geonomoid palms. The coryphoid, borassoid, caryotoid, and cocosoid palms are relatively advanced in their average values, and the lepidocaryoid palms are most advanced of all.

COMPARISON WITH NARROW TRACHEARY ELEMENTS OF THE METAXYLEM. The narrow tracheary elements of the metaxylem are either similar to or more primitive than the wide tracheary elements from the same organ. The narrowest tracheary elements of the metaxylem nearly always appear to be tracheids, on the basis of the configuration of secondary wall. The wider of the narrow tracheary elements of the metaxylem frequently have configurations of secondary wall that indicate either true scalariform perforation plates, or, at least, a series of relatively large pits.

In some specimens with simple perforation plates in the wide vessel elements, some of the narrow tracheary elements of the metaxylem (usually the wider ones) have simple perforation plates. Such cells occur in many of the roots examined and in some stems (e.g., of some coryphoid and lepidocaryoid palms), but not in petioles. The narrow tracheary elements of the metaxylem in such specimens usually contain a closely graded array of forms, from tracheid-like through scalariform configurations to simple perforation plates.

At the other extreme are specimens in which the narrow tracheary elements of the metaxylem all appear to be tracheids on the basis of the configuration of the secondary wall (e.g., petioles of many chamaedoreoid and geonomoid palms). In these specimens, the perforation plates of the wide vessels are primitive.



FIGURES 32–40. Wide tracheary elements of metaxylem. *32*, petiole of *Nypa fruticans*, × 95. End wall (arrow) is slightly curved and continues distally beyond perforation plate to tip of vessel element. *33*, petiole of *Cryosophila albida*, × 240. End wall with both perforations (right) and intervessel pits (left). Arrow indicates region where the two types of apertures intergrade. *34*, petiole of *Calyptronoma occidentalis*, × 360. End wall with perforations (right) and intervessel pits (left). Arrow indicates region where the two types of apertures intergrade. *35*, petiole of *Nypa fruticans*, × 260. End wall in which perforations do not extend to lateral margin. Arrow indicates row of pitlike aper-

DISCUSSION

THE TAXONOMIC GROUPS OF PALMS. Many of the major groups of palms differ among themselves in the form of their perforation plates, but the differences are more often average than absolute because of the variability of this character within the groups. Some of the larger major groups comprise alliances with relatively similar averages and/or ranges of variability: the alliances of the coryphoid major group (FIGURES 41–43) and of the cocosoid major group (FIGURES 42, 43), and many of those of the arecoid major group (Klotz, 1977). Some of the major groups contain groups of species of similar habit that are relatively homogeneous in the form of their perforation plates — for example, the small, slender, canelike species of chamaedoreoid palms are almost uniformly primitive in the form of their perforation plates, and the lianoid species of lepidocaryoid palms are all very advanced in this character.

STEMS OF THE PHYTELEPHANTOID PALMS. The reported absence of vessels from the rhizomatous stem of *Ammandra decasperma* may represent some kind of sampling artifact, for great difficulty was encountered in isolating tracheary elements from this specimen. The long, crooked tracheids (?) obtained occur in irregular clusters of 10 to 20 in the vascular bundles. If this species truly lacks vessels in the stem, it exemplifies what Cheadle (1943b) found in certain rhizomatous species in which vessels are lacking in the rhizomes but are present in the other organs of the plant.[3]

In the short, mostly subterranean stem of *Phytelephas macrocarpa*, Tomlinson (1961) found no vessels but only short, irregular tracheids with pointed ends and angular cross-sectional shape. In the present survey, similar results were obtained in a trunkless specimen of *P. microcarpa* within the intermediate one-third of the diameter of the stem (Klotz, 1975) except that the tracheary elements are long, and some of them exhibit regions of possible scalariform perforations on the lateral walls (FIGURE 40). However, a different collection of the same species yielded unequivocal vessels along with many tracheids from the center of the short stem. The vessel elements resemble those from the erect, emergent stems of *Phytelephas* sp. (*Moore & Dransfield 10224* — not included in the tabulations for this study) and another phytelephantoid species, *Palandra aequatorialis*.

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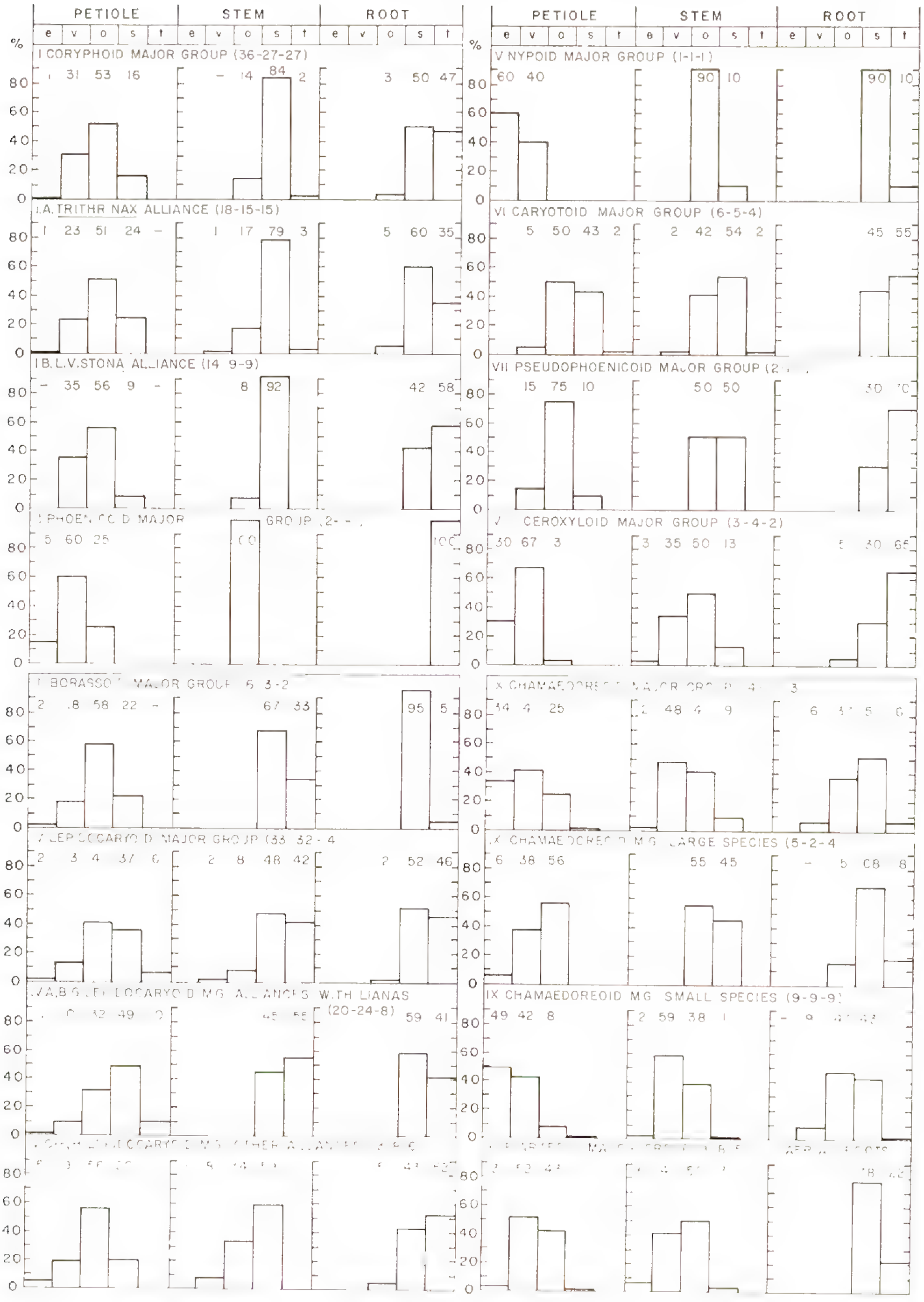
tures lateral to perforations on end wall. 36, stem of *Sindroa longisquama*, × 88. Arrow indicates long, broad ligule. 37, stem of *Elaeis oleifera*, × 88. Arrow indicates short, broad ligule. 38, stem of *Itaya amicorum*, × 160. Arrow indicates slender ligule. 39, root of *Aiphanes* sp., × 100. "Saddle-shaped" end wall. 40, tracheary element from stem of *Phytelephas microcarpa*, × 240. Arrow indicates possible perforation plate.

[3] However, a maceration from the same stem in the slide collection of P. B. Tomlinson includes tracheary elements with regions of possible scalariform perforations on the lateral walls (as in FIGURE 40).



PHYLOGENETIC IMPLICATIONS. The most primitive xylem in palms is not found in the coryphoid major group, which contains the greatest number of other primitive characters, but in more advanced groups such as the nypoid, chamaedoreoid, iriarteoid, podococcoid, and arecoid palms. In the evolutionary line comprising the pseudophoenicoid, ceroxyloid, and chamaedoreoid major groups (Moore, 1973), the small chamaedoreoid palms have the most primitive xylem, yet include the genera most advanced

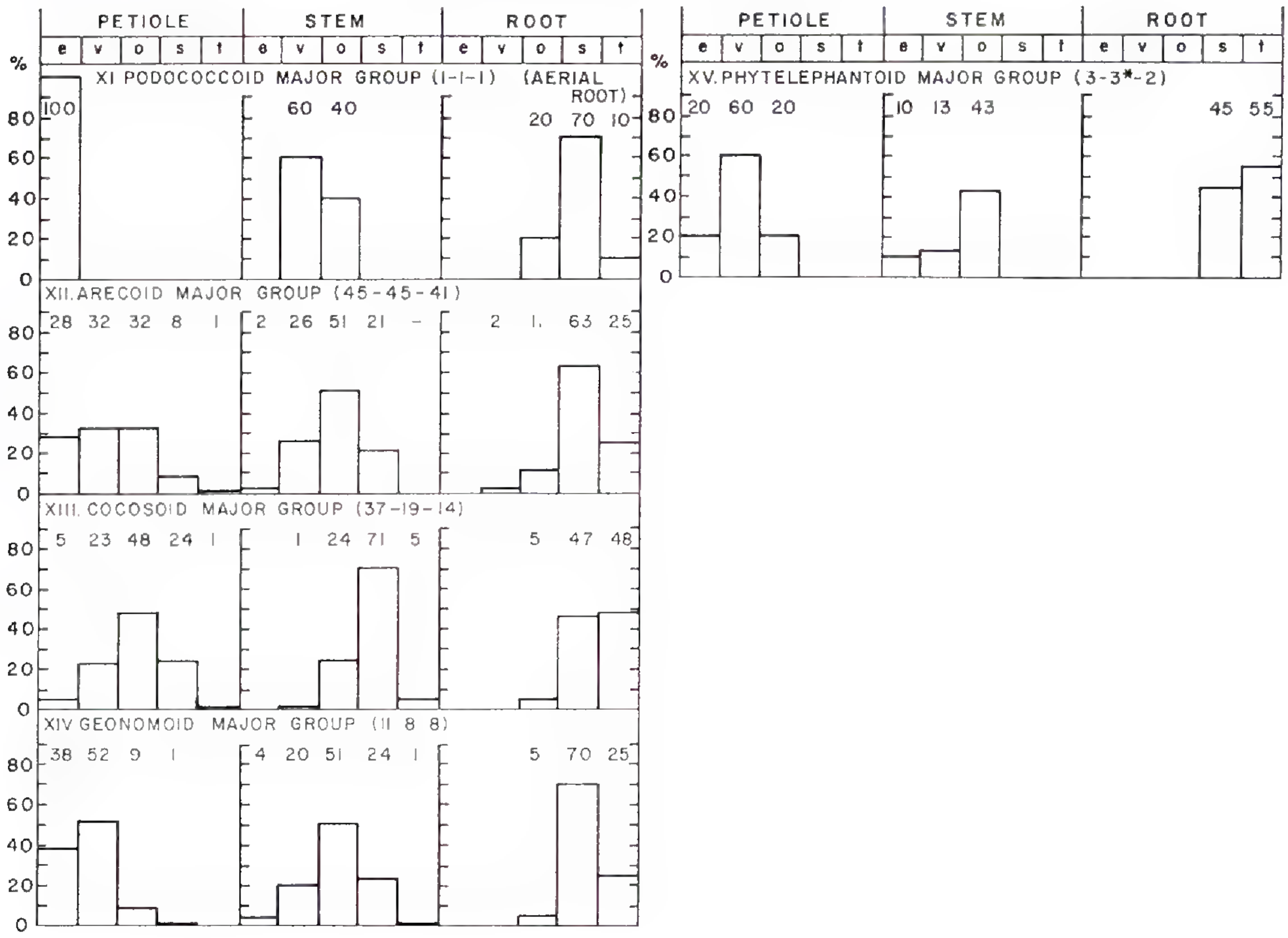


FIGURE 41. End wall slopes of wide tracheary elements of metaxylem: histograms of proportional frequencies of the five categories of slope. Proportional frequencies (as percentages) printed under their respective categories. Values of less than one percent recorded as a dash (–). Numbers of specimens examined in each group for petiole, stem, and root in parentheses. * Including *Ammandra* (= 0).

in other characters. *Pseudophoenix*, the most primitive genus in this evolutionary line, has xylem that is much more advanced than that in the small chamaedoreoid palms.

On the other hand, within the coryphoid major group, the most primitive xylem occurs in the *Trithrinax* alliance, which does contain the greatest number of other primitive features. *Nypa fruticans*, the sole species of nypoid palm, possesses a mixture of primitive and advanced features, including primitive xylem. The iriarteoid, podococcoid, and arecoid palms generally have more primitive xylem and are more primitive in other ways than are the cocosoid palms.

There is little resemblance between Moore's (1973) systematic sequence of the evolutionary lines and major groups and the sequence in the present study based on the average level of evolution of the xylem. This result is not surprising, for different selective pressures would be exerted on xylem than are exerted, for example, on the reproductive parts of the plant such as the inflorescences, flowers, and fruits. Evolution in the xylem appears to have progressed independently in the various taxonomic groups of palms.

ECOLOGICAL IMPLICATIONS REGARDING HABITAT. Carlquist (1975) hypothesized that perforation plates with few or no bars generally represent a more favorable adaptation to environmental conditions of greater average moisture demand than do perforation plates with more numerous bars that are more closely spaced. To some extent, the palms tend to display this correlation between form of perforation plates and degree of moisture demand in the environment, at least as a general trend among the major groups. For example, the coryphoid, phoenicoid, borassoid, pseudophoenicoid, and cocosoid palms include many species adapted to habitats that are very exposed (e.g., savannas) or that have low or strongly seasonal precipitation (Moore, 1973). These groups tend to have fewer, more widely spaced bars in the perforation plates than do some of the groups that are mainly adapted to more mesic habitats such as rain forest, cloud forest, or forest understory — e.g., ceroxyloid, chamaedoreoid, iriarteoid, podococcoid, arecoid, geonomoid, and phytelephantoid palms. *Nypa fruticans*, which inhabits estuaries in the humid tropics of the Old World, also fits with the latter groups regarding form of perforation plates (Carlquist, 1975). Most lepidocaryoid and caryotoid palms are adapted to tropical regions of high rainfall (Moore, 1973), but the moderately to very advanced perforation plates that characterize these species may be related to the fact that many of them inhabit forests at low elevations and must therefore tolerate the greater moisture demand that would accompany a warmer climate. However, the discrepancies that various species and higher groups of palms present with regard to these trends indicate that the relationship between form of perforation plates and adaptation to the moisture regime of the environment is not simple. For example, the lianas of the lepidocaryoid and cocosoid major groups are adapted to similar kinds of habitats yet differ markedly in the form of their perforation plates, especially in the stem. Among the arborescent species of wet lowland tropical forests, certain coryphoid palms (e.g., *Cryosophila albida*, *Itaya amicorum*, *Licuala muelleri*) have more advanced perforation plates (especially in stem and root) than do iriarteoid palms of comparable or greater size.

HABIT CATEGORIES. Few consistent relationships occur between the habits of palms and the forms of their perforation plates.[4] Among the species of lianas, the sequence of kinds of perforation plates in the organs of the plant corresponds to the modal or average condition of this character within the major group to which the species belongs. For example, only multiple perforation plates occur in the wide vessel elements of the scandent species *Chamaedorea elatior*, as in the nonscandent small chamaedoreoid palms. Species of the cocosoid genus *Desmoncus* are lianas with only multiple perforation plates in the wide vessel elements of the shoot and simple perforation plates in the wide vessel elements of the root. The sequence of kinds of perforation plates in *Desmoncus* falls within the lower part of the range of this character exhibited by the cocosoid major group. The

[4] In contrast, there are relationships between the habits of palms and the dimensions of their vessel elements, especially the diameters of the wide vessels in the stem (Klotz, 1977, 1978).

lepidocaryoid lianas are very advanced in the form of their perforation plates (FIGURES 41–43). They fall within the upper part of the range of this character in the lepidocaryoid major group.

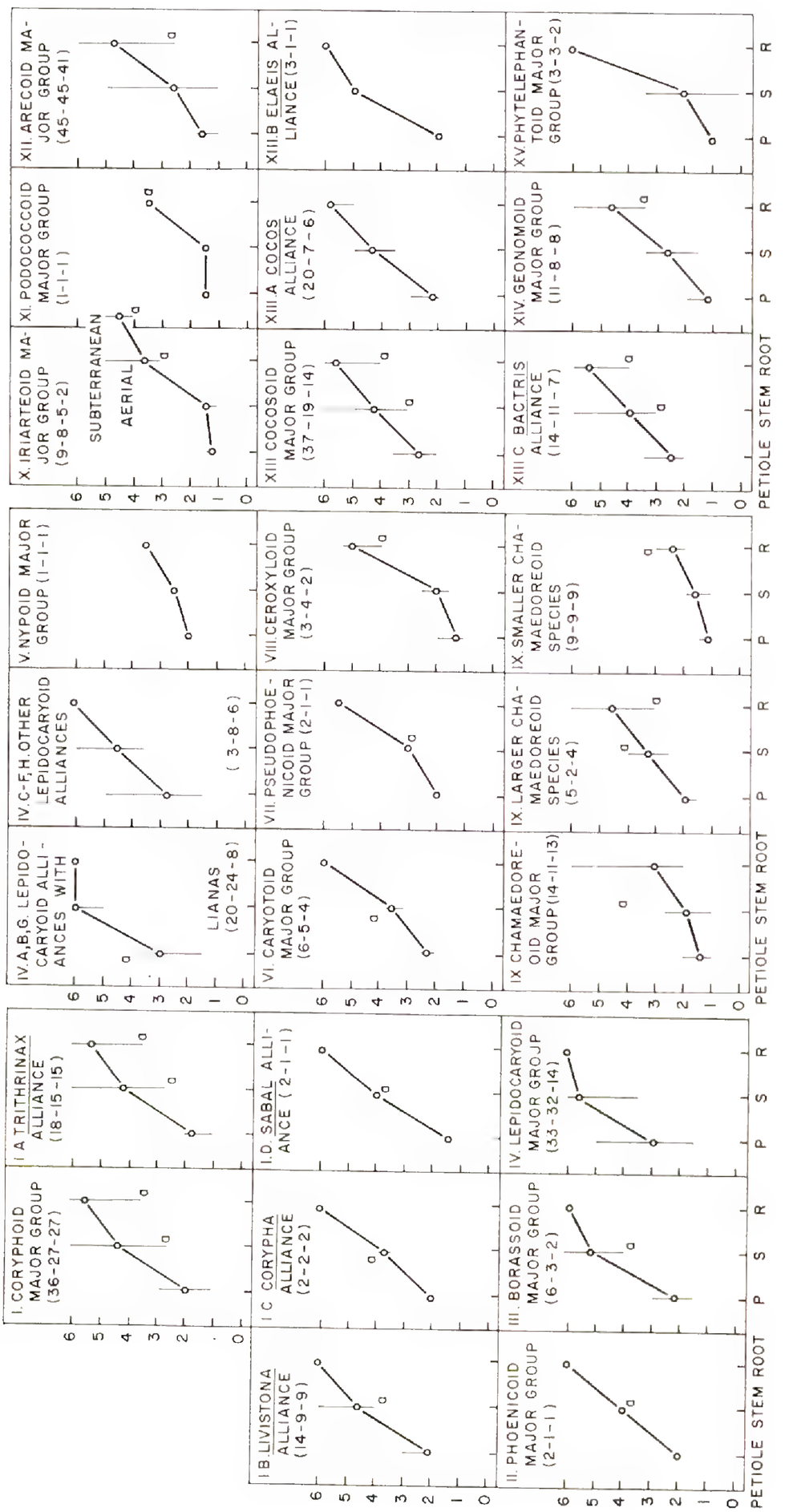
The same tendency exhibited by the lianas is also shown by the rhizomatous palms, which occur in several of the major groups. Perforation plates of the wide vessel elements of the metaxylem are all multiple in the rhizomatous stems of *Sclerosperma mannii* (arecoid), *Calyptrogyne brachystachys* (geonomoid), and *Phytelephas microcarpa* (phytelephantoid). They are mixed multiple and simple in the coryphoid palms *Rhapidophyllum hystrix*, *Licuala* sp., and *Serenoa repens*; and in the cocosoid palms *Allagoptera arenaria* and *Elaeis oleifera*. Finally, they are mostly simple in the lepidocaryoid *Eleiodoxa conferta*.

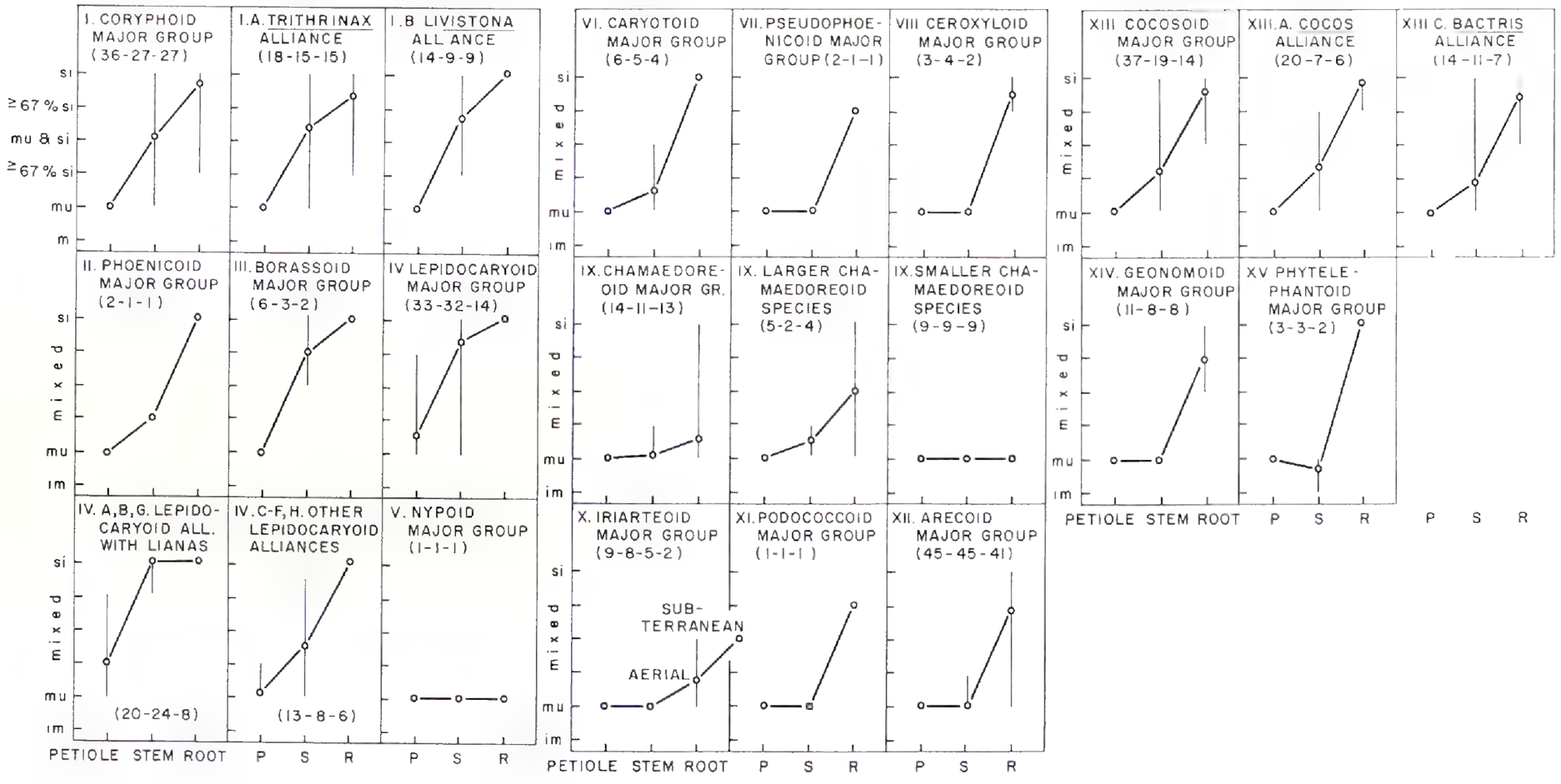
The remaining category includes all palms with erect, nonscandent stems. It is thus a very diverse group of arborescent, shrubby, and dwarf species. In this group, the small, slender species of the forest understory usually have the most primitive perforation plates within their respective major groups. This tendency is exhibited among the coryphoid palms (*Rhapis excelsa*), the lepidocaryoid palms (*Lepidocaryum* spp.), the chamaedoreoid palms (*Synechanthus* spp., *Chamaedorea* spp., *Wendlandiella polyclada*), the arecoid palms (*Reinhardtia simplex*, *Pinanga* sp., *Iguanura* sp., and others), the cocosoid palms (*Aiphanes* sp., *Bactris simplicifrons*), and the geonomoid palms (*Pholidostachys pulchra*, *Geonoma* spp.). Conversely, the most advanced perforation plates in some of the major groups occur among the larger species of those major groups — for example, *Pigafetta filaris* (lepidocaryoid); *Hyophorbe indica* (chamaedoreoid); *Manicaria saccifera*, *Roystonea* spp. (arecoid); and *Welfia georgii* (geonomoid).

DATA OF OTHER AUTHORS. Cheadle (1942) found only scalariform perforation plates in the metaxylem of leaves (22 species of palms) and inflorescence axes (6 species). In aerial stems, he found 15 species with scalariform perforation plates only and 8 species with a mixture of scalariform and simple perforation plates. In roots, all 21 species that he examined had a mixture of scalariform and simple perforation plates in the metaxylem, although the scalariform perforation plates were generally restricted to the early-matured metaxylem. The present study reports petioles that contain simple perforation plates and roots that lack simple perforation plates. Thus Cheadle's (1942) findings are similar to those of the present study except that he found fewer kinds of perforation plates within leaves and roots of palms.

Mahabalé (1959) observed the range of numbers of perforation plate bars in stems of 14 species of palms, including 8 species of *Phoenix*. Most of his data fit within the limits of the variation observed for the major groups in the present study.

Tomlinson's (1965) brief summary of his unpublished findings on perforation plates in palm stems presents a sequence for the taxonomic groups according to their average level of evolution in this character. His


I. CORYPHOID MAJOR GROUP (36-27-27)
I A TRITHRINAX ALLIANCE (18-15-15)
I B LIVISTONA ALLIANCE (14-9-9)
I C CORYPHA ALLIANCE (2-2-2)
I D SABAL ALLIANCE (2-1-1)
II. PHOENICOID MAJOR GROUP (2-1-1)
III. BORASSOID MAJOR GROUP (6-3-2)
IV. LEPIDOCARYOID MAJOR GROUP (33-32-14)
IV A,B,G. LEPIDOCARYOID ALLIANCES WITH
LIANAS (20-24-8)
IV C-F,H. OTHER LEPIDOCARYOID ALLIANCES
(3-8-6)
V. NYPOID MAJOR GROUP (1-1-1)
VI. CARYOTOID MAJOR GROUP (6-5-4)
VII. PSEUDOPHOENICOID MAJOR GROUP (2-1-1)
VIII. CEROXYLOID MAJOR GROUP (3-4-2)
IX CHAMAEDOREOID MAJOR GROUP (14-11-13)
IX. LARGER CHAMAEDOREOID SPECIES (5-2-4)
IX. SMALLER CHAMAEDOREOID SPECIES (9-9-9)
X. IRIARTEOID MAJOR GROUP (9-8-5-2)
SUBTERRANEAN
AERIAL
XI. PODOCOCCOID MAJOR GROUP (1-1-1)
XII. ARECOID MAJOR GROUP (45-45-41)
XIII. COCOSOID MAJOR GROUP (37-19-14)
XIII A COCOS ALLIANCE (20-7-6)
XIII B ELAEIS ALLIANCE (3-1-1)
XIII C BACTRIS ALLIANCE (14-11-7)
XIV. GEONOMOID MAJOR GROUP (11-8-8)
XV. PHYTELEPHANTOID MAJOR GROUP (3-3-2)
PETIOLE STEM ROOT P S R
0 1 2 3 4 5 6



FIGURES 42, 43. Specialization values of wide tracheary elements of metaxylem. 42 (above), according to author's method; 43 (below), according to Cheadle's method. Numbers of specimens examined of petiole, stem, and root, respectively, in parentheses under the name of each group.

sequence of groups is similar to the ones that are set forth in the present study (TABLES 1, 2) except that he lists the phytelephantoid palms as lacking vessels in the stem. He found the chamaedoreoid and iriarteoid palms to be "least specialized"; the "Arecoid" (including geonomoid), nypoid, and phoenicoid palms to be "unspecialized"; the caryotoid, cocosoid (including "Cocoid" and "Bactroid"), coryphoid (as "Sabaloid"), and nonscandent lepidocaryoid palms to be "moderately specialized"; and the borassoid and scandent lepidocaryoid palms to be "most specialized." Tomlinson's data on the forms of perforation plates in various species of palms (Tomlinson, 1961; 1966; 1969; unpublished data) generally agree with the trends expressed for the major groups in the present study.

TYPES OF VASCULAR BUNDLES. In their survey of monocotyledons, Cheadle and Uhl (1948) found that as the wide vessel elements of the metaxylem became more advanced, "they became larger in relation to the remaining elements in the metaxylem." In petioles of palms, the most primitive wide vessel elements (i.e., those with the narrowest perforations) occur in bundles of types IIIA and IV rather than type I, which is considered to be the most primitive bundle type. The species with type I bundles predominating in the petiole have wide vessel elements of metaxylem in which the bars of the perforation plates tend to be slightly more widely spaced (Klotz, 1977). However, this exception to the relationship stated by Cheadle and Uhl (1948) is relatively minor. The present observations in palms generally support the conclusions of these authors.

SUMMARY

Perforation plates of the wide vessels of metaxylem from the petiole (209 species), the central part of the stem (169 species), and the root (136 species) were examined in representative species from all of the major groups of palms. In nearly all of the species examined, the bars of the perforation plates are most closely spaced in the petiole, most widely spaced in the root, and intermediate (or else similar to either petiole or root) in the stem. End walls of the wide vessel elements are most oblique in the petiole, least oblique in the root, and intermediate in the stem. Differences in the form of the perforation plates among the taxonomic groups are mostly average or partial rather than absolute. *Nypa* has multiple perforation plates in all three organs. Iriarteoid and most chamaedoreoid palms have multiple perforation plates in all organs, but some species also have simple perforation plates in the roots. Ceroxyloid, geonomoid, most arecoid, and most phytelephantoid palms have either simple or mixed multiple and simple perforation plates in the roots and only multiple perforation plates in the shoots. Caryotoid, most cocosoid, and most coryphoid palms have simple perforation plates in the roots, multiple or mixed multiple and simple perforation plates in the stems, and multiple perforation plates in the petioles. Lepidocaryoid palms have multiple, mixed multiple and simple, or simple perforation plates in the stems, and multiple or mixed multiple and simple perforation plates in the

petioles. The form of the perforation plates is not strictly correlated with habit. For example, the lepidocaryoid lianas all have simple perforation plates in the stems, but only multiple perforation plates occur in the stems of the cocosoid and chamaedoreoid lianas. The form of the perforation plates shows only partial or inconsistent correlation with environmental moisture regime and with evolutionary advancement in other characters.

ACKNOWLEDGMENTS

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GENERIC LIMITS IN THE XEROTEAE (LILIACEAE SENSU LATO)

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THE GENUS *Lomandra* Labill., variously placed in the Liliaceae Juss. (e.g., Engler, 1888; Krause, 1930), Juncaceae Juss. (Bentham, 1878, 1883), Xanthorrhoeaceae Dumort. (Melchior, 1964; Airy Shaw, 1973; Hutchinson, 1973), or Lomandraceae Lotsy (including *Xanthorrhoea*; Lotsy, 1911), currently contains about forty-three species. Forty-one of these species are endemic to Australia, growing mostly in the south and east, one species, *L. banksii*, is known from Australia (Queensland), New Caledonia, and southern New Guinea, while a single species, *L. papuana*, has hitherto been known from a single collection made in northeast New Guinea.

During a collecting trip with Y. Lelean (Division of Botany, Lae, Papua New Guinea) in the mountains of New Britain in 1973, the author was fortunate enough to collect a rather inconspicuous liliaceous plant with the facies of a species of *Dianella*, but with asymmetric, capsular fruits; another collection was made independently by J. Croft and P. Katik. This plant could not readily be placed in a genus, but Professor C. G. G. J. van Steenis, of Leiden, drew my attention to *Aet & Idjan 24*, from West New Guinea, obviously the same taxon as the New Britain plant, and identified as *Lomandra*. The New Britain and West New Guinea plants were found to be conspecific with *L. papuana*, a species hitherto known only from a single fruiting collection made in the Madang Province of Papua New Guinea. Lauterbach (1913) tentatively assigned *L. papuana* to section EULOMANDRA (correctly LOMANDRA) series Sparsiflorae. The unusual characters of *L. papuana*, which had caused my initial difficulties in naming the plant, prompted a survey of the differences between *Lomandra* and related genera, the results of which are presented below.

GENERA ASSOCIATED WITH LOMANDRA

Seven genera have often been associated with *Lomandra* in whatever family it has been placed: *Acanthocarpus* Lehm. (1 species), *Chamaexeros* Bentham (3 species), *Baxteria* R. Br. (1 species), *Calectasia* R. Br. (1 species), *Dasypogon* R. Br. (2 species), *Kingia* R. Br. (1 species), and *Xanthorrhoea* J. E. Sm. (ca. 15 species).

Bentham (1878) divided these genera among three tribes in the Juncaceae. The Xeroteae Bentham, including *Xerotes* (a synonym of *Lomandra*), *Chamaexeros*, and *Acanthocarpus*, were characterized by the small perianth, usually scarious or hyaline, rarely petaloid; dorsifixed anthers; and 3-celled ovary with one laterally attached ovule per loculus. The Xanthorrhoeae Bentham included *Xanthorrhoea* and *Dasypogon*, and were distinguished by the perianth, of which the outer whorl was glumelike and

the inner whorl thin and scarious or petal-like; the dorsifixed anthers; the variable ovary; and the stem, which was either short, thick, and hard, or elongated and woody. The Calectasieae Bentham, including *Kingia*, *Baxteria*, and *Calectasia*, were distinguished by the rigid, sometimes colored, perianth; the basifixed anthers; and the ovary, which had three ovules. Subsequent classifications are variations of this arrangement.

Bentham (1883) merged the Xanthorrhoeae with the Xeroteae. The classification of Engler (1888; in the Liliaceae, subfamily Asphodeloideae), followed that of Bentham, except that *Dasypogon* was the sole genus in a new tribe, the Dasypogoneae, characterized by a 1- or incompletely 3-locular ovary, basally attached ovules, and a single-seeded, indehiscent fruit. In the Lomandreae, which had the circumscription of the Xeroteae *sensu* Bentham (1883), *Chamaexeros* was included in *Acanthocarpus*; the Calectasieae were unchanged. Krause (1930) followed Engler, but reinstated the genus *Chamaexeros*; Fitzgerald (1903) had earlier removed *Xerotes turbinata* Endl. to a monotypic genus, *Hensmania* Fitzgerald, which Krause (1930) included in the Liliaceae-Asphodeloideae-Johnsonieae.

Fahn (1954, 1961) examined the leaf anatomy, and, less comprehensively, the anatomy of the stem and root, of a great majority of the species in the eight genera, and suggested that the genera fell into four groups: *Lomandra-Chamaexeros-Acanthocarpus*, *Xanthorrhoea*, *Dasypogon-Calectasia*, and *Kingia-Baxteria*. However, he included *Hensmania* in *Lomandra* (as *L. turbinata*), but did not find anything distinctive in its anatomy, so his conclusions should be treated with caution.

A recent palynological survey of forty-two species from all eight genera (Chanda & Ghosh, 1976) shows a very considerable range of variation of the pollen both between and within (especially in *Lomandra*) the genera. Chanda and Ghosh also recognized four groups of genera; these were, however, mostly differently circumscribed from those of Fahn. Although they placed *Lomandra*, *Chamaexeros*, and *Acanthocarpus* together, they noted that *L. micrantha*, *L. leucocephala* subsp. *leucocephala*, and *L. endlicheri* should be excluded from the Lomandraceae (i.e., the rest of *Lomandra* plus the two other genera) on palynological grounds (*op. cit.*, p. 550), and placed with *Aphyllanthes* of the Liliaceae, an advanced member of the family (see also Erdtman, 1966). They did not consider morphological characters, but noted that the groups that they recognized did not correlate very well with those recognized by Fahn (1954, 1961) on anatomical grounds.

Other recent work on these genera is that by Lee (1966, 1972), who described a few taxa in *Lomandra* and *Xanthorrhoea*, and Kuchel (1976), who described a third species in *Chamaexeros*. Burbidge (1963) and Airy Shaw (1973) recognize the same genera as did Bentham (1878). Hamann (1961, pp. 712–714) briefly discusses the relationships of the Xanthorroeaceae.

All eight genera agree in their xeromorphic facies and their often rather tough perianth parts; in addition, the stem tends to be stout and erect. However, there is considerable variation in inflorescence, in details

of the perianth, and in stamens, ovary, and fruit, as well as in anatomy (Fahn, 1954, 1961) and palynology (Chanda & Ghosh, 1976). These genera may not all be particularly closely related, but *Lomandra*, *Chamaexeros*, and *Acanthocarpus* are three genera which appear to be related and which have a number of characters in common.

Plants in these three genera are usually rather small, although of varied habit. The inflorescence is many flowered. The tepals are small, often rather tough (but not woody), usually similar in shape and size, and persistent at the base of the capsule, becoming indurated. The six anthers are dorsifixed. The completely 3-locular ovary has one, rarely two, ovules attached to the middle of the axis of the ovary (in one species at the apex); the style is not inflated. The 1- to 3-seeded capsule is loculicidal. The seeds have a thin, dull, brown to yellowish brown testa which is often finely reticulate because of the prominence of the anticlinal cell walls (FIGURE 5), and the endosperm, although oily, is tough. The micropyle faces the bottom of the ovary loculus, 90° from the point of attachment of the seed to the placenta (this position will be called basal, since the micropyle is at the bottom of the long axis of the seed). The embryo is straight or slightly curved. There is also substantial agreement between the genera in lamina anatomy. The palisade mesophyll, when present, is bifacial, and there are raphides in some cells. The fibers surrounding the vascular bundles join the epidermis on at least one side of the lamina in all except two species, the vascular bundle as a whole being dorso-ventrally elongated in all species. There is no lignified hypodermis (details from Fahn, 1954, 1961; Kuchel, 1976).

Xanthorrhoea, one of the genera that has been included in the same tribe as *Lomandra*, differs from the *Lomandra* group in several characters. *Xanthorrhoea* is often quite a large plant, and the base of the leaf widens abruptly (rare in the *Lomandra* group). The inflorescence structure is very complicated (Waterhouse, 1967), but the ultimate bracts lack the regular arrangement of those of species of the *Lomandra* group (see below). The inner perianth whorl is somewhat larger and more petaloid than the outer, a condition rare in the *Lomandra* group, although occurring there (e.g., in *L. juncea*). The seed has a black, crustaceous, almost shiny, and minutely bullate testa; the embryo lies almost horizontally across the seed, being only slightly curved in the vertical plane. The anatomy of the lamina is very distinctive. The hypodermis is sclerified, and the center of the leaf is filled with pithlike tissue. In this pith are radially arranged (i.e., as in the stem), V-shaped vascular bundles with phloem occupying the arms (see Fahn, 1954, 1961). Chromosome numbers in *Xanthorrhoea* are consistently $n = 11$; those of *Lomandra* are more variable (Briggs, 1966), being based on $n = 7$ and $n = 8$ (Lee, 1966). Chromosome numbers in other genera of the Xeroteae are unknown.

Dasypogon, the other genus which has been included in the Xeroteae, has a capitate inflorescence superficially similar to that of some species of *Lomandra*, but with a different arrangement of bractlike structures and flowers (compare FIGURE 2, b, with FIGURE 4, g, h). There are major

differences in the flower: the tepals are large, the outer three being connate and woody toward the tips while the inner three are free and rather delicate (in *Lomandra*, any connation of the tepals affects both series); the ovary is imperfectly 3-locular, with 3 basal ovules; the style is swollen. The fruits are reported to be 1-seeded and indehiscent (Bentham, 1878). In anatomy, *Dasypogon* differs from members of the *Lomandra* group: it lacks raphide cells in the mesophyll, it has only abaxial palisade tissue, and it has vascular bundles in groups of three surrounded by a common fiber sheath, the whole being more or less circular in transverse section and not reaching the epidermis (Fahn, 1954, 1961).

The other genera which have consistently been placed near *Lomandra*, but not in the same tribe, are also markedly different from the *Lomandra* group in anatomy (Fahn, 1954, 1961) and in many details of inflorescence, flower, and fruit. *Hensmania turbinata* (Endl.) Fitzgerald, once included in *Xerotes* (see above), differs from the genera once included in the Xanthorrhoeaceae in having a fleshy perianth, only three stamens with the thecae separated by a broad connective, and black, nitid, carunculate seeds with a soft endosperm. The monotypic genus *Aphyllanthes* (*A. monspeliensis* L. is the only species), which Chanda and Ghosh (1976) considered to be similar in pollen type to *Lomandra micrantha*, *L. leucocephala* subsp. *leucocephala*, and *L. endlicheri*, is also a very different plant from both the Xanthorrhoeaceae as a whole and the *Lomandra* group in particular. The individual flowers of the solitary to 3-flowered, capitate inflorescence are surrounded by a spiral involucre of 4 to 5 "bracts" that are connate at the base. The perianth is large, brightly colored, and fleshy, and the black seeds have a minutely bullate testa and a soft endosperm. *Aphyllanthes* also has bisexual flowers, a long style, and a stigma that has three spreading (rather than recurved) lobes, all additional differences between it and the three species of *Lomandra* mentioned, as well as most other species of the genus (see below).

Lomandra papuana, however, agrees with all the details in the description given above for members of the *Lomandra* group, except that its embryo is strongly curved, and so further discussion will be restricted to a comparison of *L. papuana* with *Lomandra*, *Chamaexeros*, and *Acanthocarpus*. Unqualified mention of *Lomandra* may be taken to include all species currently included in the genus *Lomandra* except *L. papuana*; the Xeroteae will be used to refer only to these four taxa, essentially the same circumscription as when it was originally used (Bentham, 1878).

VARIATION OF CHARACTERS AT THE GENERIC LEVEL WITHIN THE XEROTEAE

The main morphological differences between *Lomandra papuana*, *Chamaexeros*, *Acanthocarpus*, and the other species of *Lomandra* are summarized in TABLE 1. The characters are discussed below, and the anatomy of *L. papuana* is described.

TABLE 1. **Variation of some characters in Lomandra, L. papuana, Chamaexeros, and Acanthocarpus.***

CHARACTER	*Lomandra*	*Chamaexeros*	*Acanthocarpus*	*Lomandra papuana*
LEAF MARGIN	prickly, rarely scarious or almost smooth	scarious	prickly	smooth
LEAF BASE AURICULATE	rarely	−	+	−
FLOWER CLUSTERS IN INFLORESCENCE CLEARLY CYMOSE	+ −	−	+	+
FLOWER TYPE ON SINGLE PLANT	usually [♂], [♀] rarely [☿], [♂ ♀], [☿ ♂], or [☿ ♀]	☿	☿	☿
STIGMA PROMINENTLY RECURVED-TRIFID	+	−	−	−
STYLE LESS THAN TWICE AS LONG AS OVARY	+	−	−	+
NUMBER OF OVULES PER LOCULUS	1	2	1	2
POSITION OF OVULES IN LOCULUS	median	median	near apex	median
SEED FOVEATE	−	−	−	+
EMBRYO ± STRAIGHT, MICROPYLE BASAL	+	+	+	−
FRUIT WITH SPINES	−	−	+	[−]

* Explanation of symbols: +, character state as mentioned; −, character state other than that mentioned; [−], character state approaching that mentioned.

LEAF MARGIN. *Lomandra papuana* has a leaf without papillae, spines, or scarious margin (this last is present only at the base). All species of *Chamaexeros* have a white, scarious margin to the leaf that runs the length of the leaf, as does *L. leucocephala* (especially prominent in subsp. *leucocephala* — the decurrent leaf base of Lee, 1966), but there is an important difference between them. *Chamaexeros* lacks fiber strands in the leaf margin. The margins of *C. fimbriata* and *C. macranthera* consist of polygonal cells adjacent to the green part of the leaf and an irregular fringe of cells elongated at right angles to the leaf; the margin of *C. serra* consists almost entirely of the latter type of cells. *Lomandra leucocephala*, on the other hand, has fiber strands in the leaf margin, and the rest of the cells are elongated parallel to the long axis of the leaf. The closest approach to the *Chamaexeros* type of leaf margin in *Lomandra* perhaps occurs in species like *L. sororia*. That species has small, earlike flaps of tissue along the leaf edge; these flaps have cells elongated at right angles to the long axis of the leaf.

LEAF BASE. Auriculate leaf bases are rare in *Lomandra*, although they occur in *L. obliqua* (Lee, 1972, *figure 1*); normally the leaf widens only gradually toward the base.

INFLORESCENCE TYPE. No previous attempt has been made to interpret the inflorescences in the Xeroteae, mainly because of their great reduction and numerous parts. The diagrams given here must be considered merely as a preliminary contribution to the subject, based as they are on rather limited observations of herbarium material; developmental studies are sorely needed.

The nomenclature of the parts is a rather difficult question. Lee (1966) used the term "cluster bracts" for pointed, leaflike bracts subtending both branches and clusters of flowers, and "bracts" for all the other structures. This is somewhat of an oversimplification. In a large cluster of flowers, there may be all intermediates between leaflike bract structures (cluster bracts) and broad structures rounded at the apex (see also Lee, 1966, p. 16). These broader bractlike structures may split down the middle (see also Lee, 1966), resulting in two apparently independent bracts; Arber (1925) gives details of the effect that pressure during development may have on the shape of prophylla in monocotyledons, although it should be noted that Stebbins (1974, and references therein) has a different interpretation of prophylla. In some cases the terminal cluster of flowers may lack cluster bracts, while the clusters along the stem may be subtended by them (e.g., *Lomandra banksii*, *L. multiflora*). The terms "bract" and "bracteole" are impossible to use confidently for similar reasons; there may be a variable number of "bracts" surrounding the flower, and the "bract and bracteole" of a flower may turn out to be the lowest two bracts surrounding the single flower of a reduced cymose inflorescence. There are sometimes irregular changes in the position of insertion of the

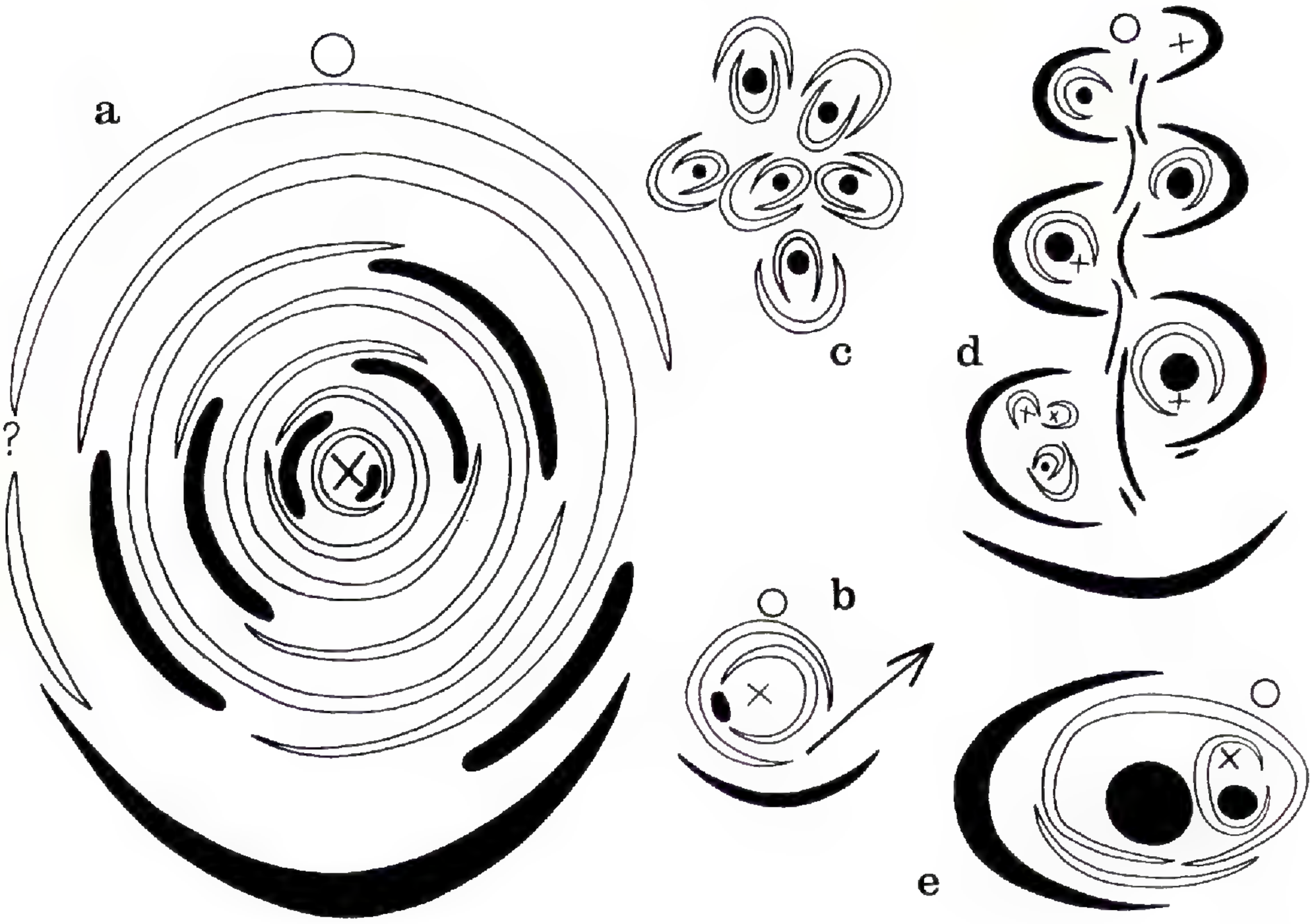

FIGURE 1. Inflorescence structure (diagrammatic). a, b, *Lomandra papuana*: a, axillary flower cluster (*NGF 41283*); b, axillary cluster showing origin of a lateral branch (*NGF 41283*). c, *Chamaexeros fimbriata*, terminal cluster (*Salisbury 31*). d, e, *Lomandra hastilis*; d, axillary cluster near top of inflorescence (*George s.n.*, 11 July 1961); e, subcluster from axillary branch near base of inflorescence (*Canberra Botanic Gardens 22976*, coll. *Philips*, 23 Oct. 1972). (Filled crescents = cluster bracts; unfilled crescents = bractlike structures; filled circles or ovals = flowers; unfilled circles = inflorescence axis; parallel lines = axis of cluster; arrow = inflorescence branch; x = structure unclear.)

various bractlike structures (see FIGURES 1, a; 2, a), but these must be treated with caution because of distortions in the dried material.

This being said, it has been possible to establish some taxonomically important variation in inflorescence type. The terms "bract," "bracteole," and "cluster bract" are used despite the caveats entered above. The term "cluster bract" denotes a bractlike structure that subtends a cluster of flowers along the stem, although the cluster may be reduced to a single flower.

Lomandra papuana Lauterbach. The inflorescence axis is fairly long (about 30 cm.) and is irregularly branched. There are small flower clusters both at the branching points and along the unbranched axis, especially toward the apex; the clusters are subtended by cluster bracts. These clusters are clearly cymose (FIGURE 1, a) and consist of bracts which successively subtend and enclose both the terminal flowers and the rest (the younger part) of the cluster. In the clusters dissected, the flowers arose along three axes; although alternation between the axes was not always regular, this may have been caused by distortion of the dried ma-

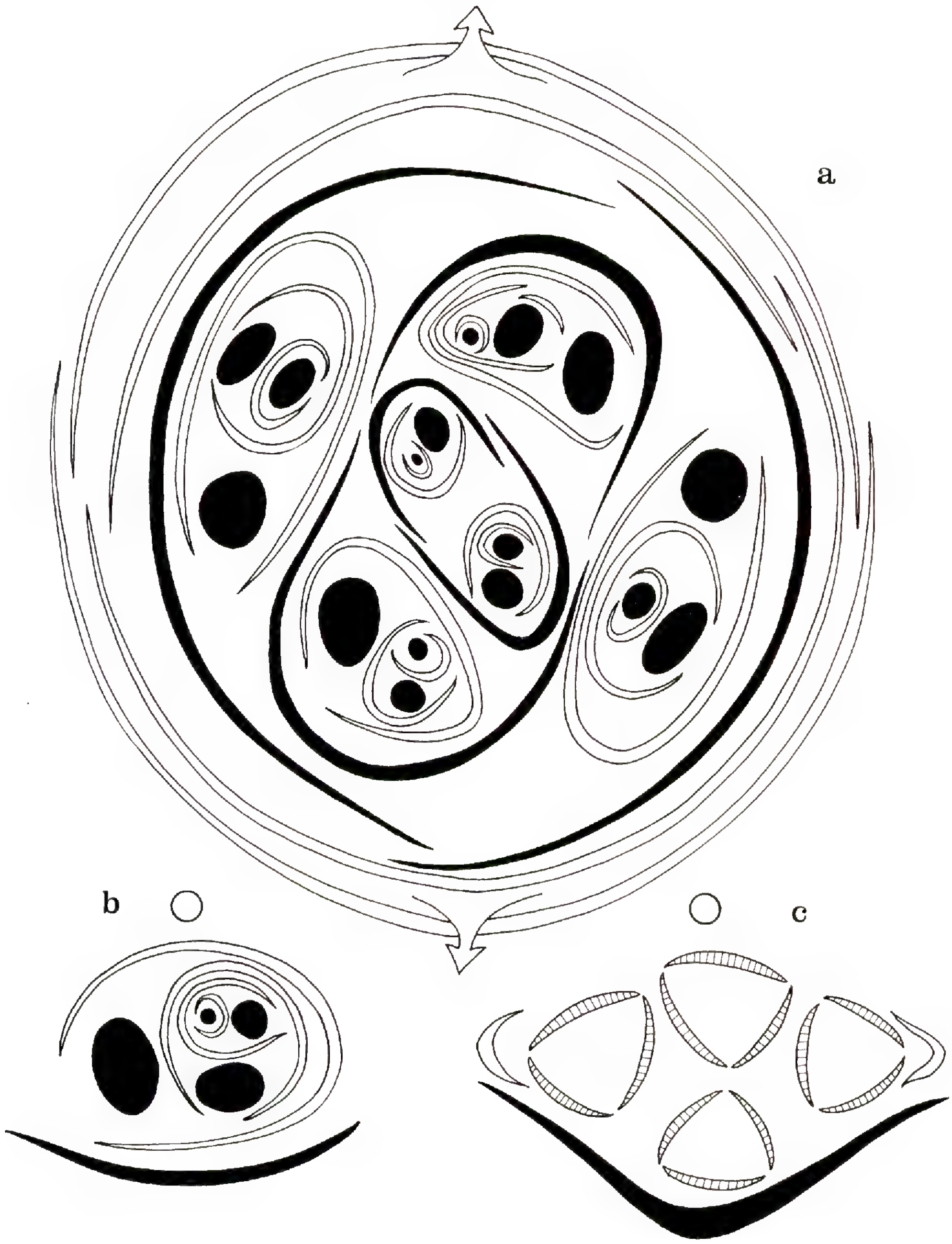

FIGURE 2. Inflorescence structure (diagrammatic). a, b, *Acanthocarpus preissii*: a, complete terminal inflorescence (*Drummond 304*); b, lowermost flower cluster of well-developed inflorescence (*Drummond 304*). c, *Dasypogon hookeri*, flower cluster (*Wilson 274*). (Filled crescents = cluster bracts; unfilled crescents = bractlike structures; crosshatched crescents = outer whorl of tepals; filled circles = flowers; unfilled circles = inflorescence axis; arrows = vegetative shoots developing from axillary buds.)

terial. Branches with racemose growth bearing further cymose clusters may develop from within the cluster (FIGURE 1, b). Each cluster is clearly long-lived, flowers probably developing successively for more than

six months, with pedicels of fallen fruits, ripe fruits, and flowers occurring in the one cluster.

Acanthocarpus. The inflorescence in the sole species of the genus, *Acanthocarpus preissii* Lehm., is basically similar to that of *Lomandra papuana*. However, the inflorescence axis is very short, and what appears to be a single, terminal cluster is in fact made up of several clusters (FIGURE 2, a), each with a cymose structure. The cymose structure of the individual clusters is clearly seen in the larger inflorescences (FIGURE 2, b). The inflorescences are not notably long-lived. As in *L. papuana*, the whole inflorescence is racemose, and the youngest clusters are borne in the distal part of the inflorescence.

Chamaexeros. *Chamaexeros macranthera* Kuchel, *C. serra* (Endl.) Bentham, and *C. fimbriata* (F. Mueller) Bentham have similar inflorescence structures, although superficially they are very different. The flowers are aggregated into clusters, each flower being surrounded by two bractlike structures, possibly bract plus bracteole, inserted opposite each other (FIGURE 1, c). No cluster bracts associated with the flower clusters were seen, but there are bracts along the inflorescence axis of *C. serra* which subtend the branches of the inflorescence.

Lomandra.[1]

Lomandra section CEPHALOGYNE (Bentham) Engler. The inflorescence structure in species of this section is very uniform. Each flower is subtended by two bractlike structures, "bract" plus broad, opposite or subopposite "bracteole," with or without associated cluster bracts. Pistillate inflorescences consist of a single, terminal head, and the cluster bracts subtend 1 to 4 flowers (FIGURE 4, c–e; note orientation of flower in FIGURE 4, e); in staminate inflorescences there are several clusters of flowers along the inflorescence axis, generally with associated cluster bracts (FIGURE 4, h), while the terminal clusters of flowers may lack cluster bracts. Both the clusters and the inflorescence axis in section CEPHALOGYNE appear to be racemose.

Species examined: *Lomandra elongata* (Bentham) Ewart, *L. glauca* (R. Br.) Ewart subsp. *glauca* and subsp. *collina* (R. Br.) A. Lee, *L. obliqua* (Thunb.) Macbride, *L. rupestris* (Endl.) Ewart, *L. suaveolens* (Endl.) Ewart.

[1] Bentham (1878) described *Xerotes* section SCHOENOXEROS Bentham (= *Lomandra* section SCHOENOLOMANDRA Engler) because it was thought that the barren stems of the included species (*L. spartea, L. juncea*) were rushlike, while the fertile stems had only sheathing scales at the base. These so-called stems are leaves (see also Fahn (1954), who was unaware of speculations as to the nature of these organs, but who found no anatomical characters leading him to doubt that they were leaves), and often have a small sheath at the base. Similar terete leaves may also be found in *L. cylindrica, L. sororia*, and *L. micrantha* (also noticed by A. T. Lee, pers. comm.). *Lomandra spartea* will be discussed under section LOMANDRA; *L. juncea* under section TYPHOPSIS. Both *L. spartea* and *L. juncea* have inverted vascular bundles in the leaf (see Fahn, 1954), but it is not known whether the terete leaves of these other (unrelated) species also have such inverted bundles. *Lomandra dura*, with flat leaves, has inverted bundles.

Lomandra section MACROSTACHYA (Bentham) Engler. The inflorescence is a "spike" bearing numerous condensed spikelet-like clusters. Each spikelet is subtended by a single cluster bract (FIGURE 1, d), and the flowers near the top of the spikelet appear to have a bract and a bracteole associated with them. However, even in the spikelets near the top of the inflorescence, the lower flowers are associated with more numerous bractlike structures (FIGURE 1, d), and lower down the inflorescence the bottom flower of a spikelet is replaced by a group of flowers which have a cymose arrangement of parts (FIGURE 1, e), so the "bract plus bracteole" represents a reduced, probably cymose, partial inflorescence.

Species examined: *Lomandra hastilis* (R. Br.) Ewart (the only species in the section).

Lomandra section TYPHOPSIS (Bentham) Engler. Elucidation of the inflorescence structure of the two species included here is made difficult by the fact that the bractlike structures are divided almost to the base into numerous hairs. Both species have flowers aggregated into dense heads. In *Lomandra leucocephala* the cluster bracts are prominent and subtend a number of flowers; each flower is completely surrounded by hairs which apparently represent two or more bractlike structures. In *L. juncea* the cluster bracts are less prominent, and there appear to be two bractlike structures surrounding each flower.

Species examined: *Lomandra leucocephala* (R. Br.) Ewart subsp. *leucocephala* and subsp. *robusta* Lee, *L. juncea* (F. Mueller) Ewart (possibly only superficially similar to the preceding species).

Lomandra section LOMANDRA (*Eulomandra* Engler, *Euxerotes* Bentham). There are about thirty-two species belonging to this section. Bentham (1878) placed the eighteen species that he recognized in three series, based on whether or not the flowers were in clusters and whether or not they were sessile. Most of the species that were included in *Xerotes* section EUXEROTES (properly XEROTES) series Fasciculatae Bentham and series Sparsiflorae Bentham have clusters which appear to be similar in structure (group A), although varying as to how they are disposed on the inflorescence axis (singly or in whorls). Members of series Glomeratae Bentham, as well as *Lomandra spartea* and *L. multiflora* (the last was placed in series Fasciculatae), have a somewhat different inflorescence structure (group B).

Group A. The flowers are borne singly (or mostly so) along the axis (Sparsiflorae: FIGURE 3, a–m), or in clusters which are in turn in whorls (Fasciculatae: FIGURE 3, o–w). The inflorescences of a number of the species in the former series appear to be simply racemose, with the bracteoles laterally placed (the exact position of the bracteole is uncertain — compare FIGURE 1, a, with *figures 78* and *83* in Eichler, 1875). However, further bractlike structures, and even flowers, may develop in association with these "bracteoles" (FIGURE 1, h, m, n). This suggests that the racemes and once-branched panicles of these species are derived from more complexly branched inflorescences perhaps with cymose partial in-

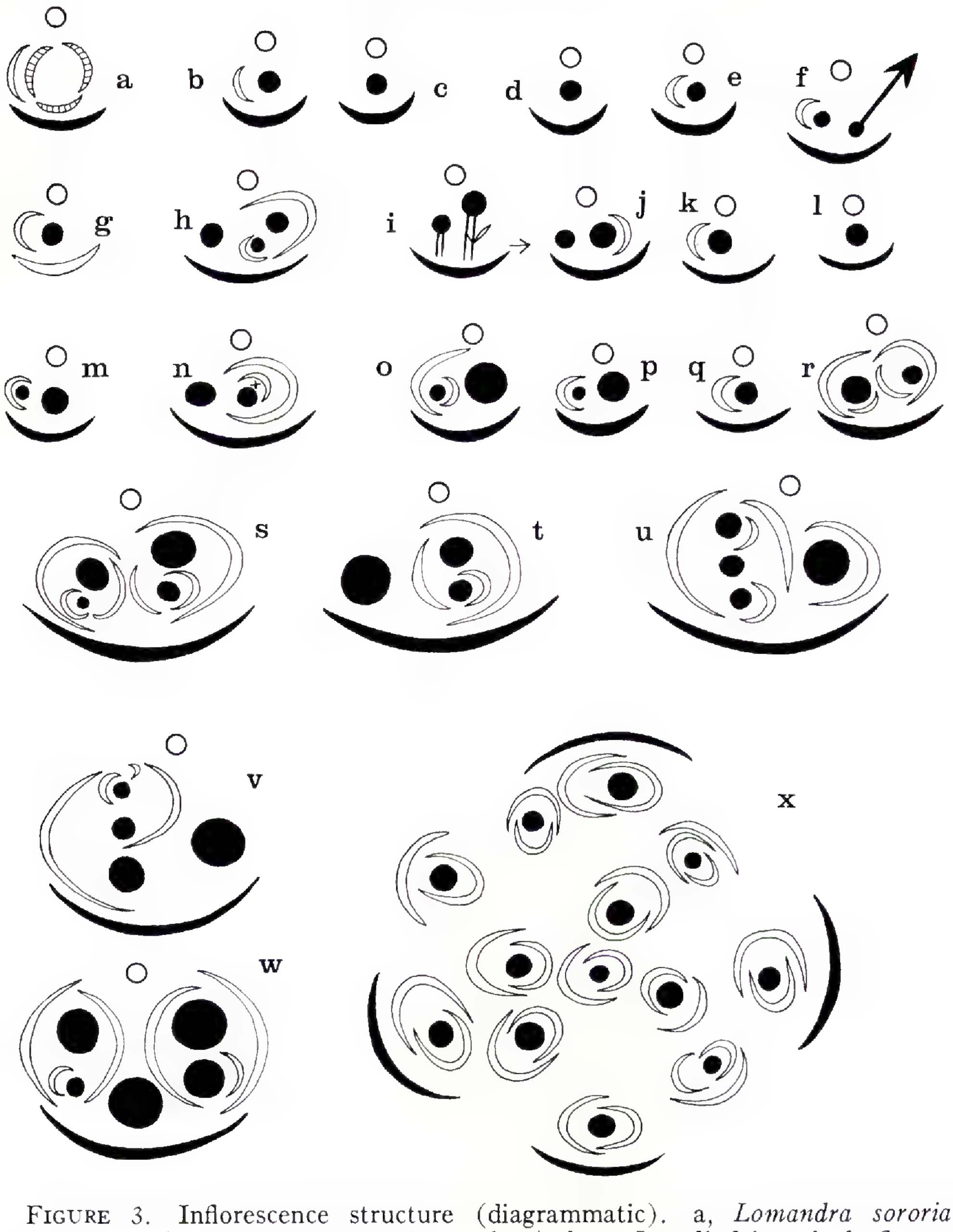

FIGURE 3. Inflorescence structure (diagrammatic). a, *Lomandra sororia*, single flower (*AD 96415025*, staminate plant). b, c, *L. cylindrica*, single flowers (*NSW 49111*, staminate plant). d–f, *L. filiformis*, single flowers: d, usual; e, rare; f, with inflorescence branch (*Clemens 44542*, staminate plant). g, h, *L. effusa*, axillary flower (clusters): g, usual; h, rare (*Pritzel 392*, staminate plant). i–l, *L. fibrata*, axillary flowers (*AD 95941052*, pistillate plant). m, n, *L. micrantha*, axillary flower clusters (*Drummond 809*, staminate plant). o–u, *L. endlicheri*: o–r, individual axillary flower clusters (*Royce 3059*, pistillate plant); s–u, three flower clusters forming a single whorl (*Pritzel 361*, staminate plant). v, *L. preissii*, axillary flower cluster (*Wilson 3728*, staminate plant). w, *L. purpurea*, axillary flower cluster (*Andres s.n.*, Oct. 1903, staminate plant). x, *L. montana*, terminal cluster (*NSW 88924*, pistillate plant). (Filled crescents = cluster bracts; unfilled crescents = bractlike structures; crosshatched crescents = outer whorl of tepals; filled circles = flowers; unfilled circles = inflorescence axis; arrows = inflorescence branches.)

florescences. The flower clusters of species in series Fasciculatae seem to be similar to, but more complex than, those of series Sparsiflorae (FIG-

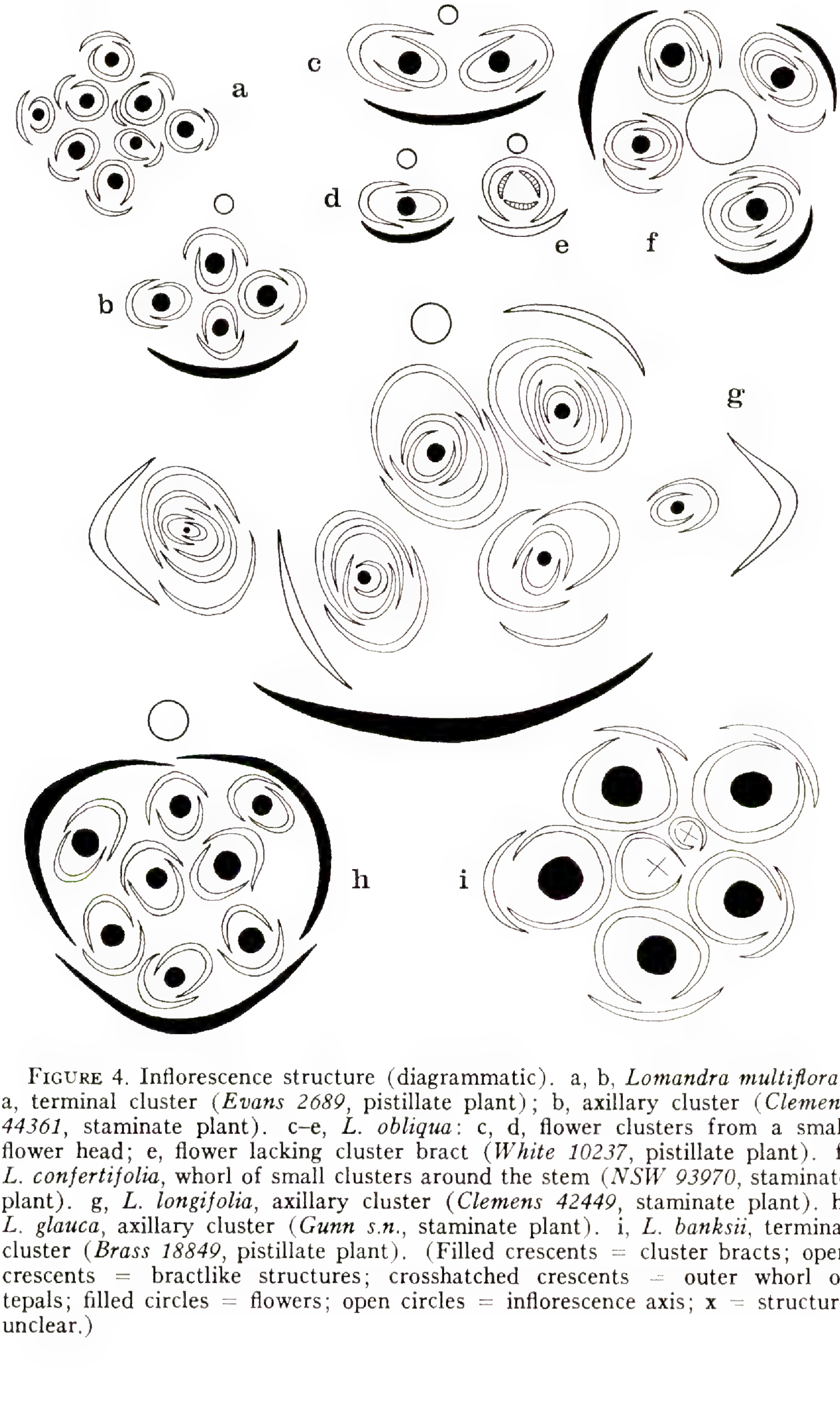

FIGURE 4. Inflorescence structure (diagrammatic). a, b, *Lomandra multiflora*: a, terminal cluster (*Evans 2689*, pistillate plant); b, axillary cluster (*Clemens 44361*, staminate plant). c–e, *L. obliqua*: c, d, flower clusters from a small flower head; e, flower lacking cluster bract (*White 10237*, pistillate plant). f, *L. confertifolia*, whorl of small clusters around the stem (*NSW 93970*, staminate plant). g, *L. longifolia*, axillary cluster (*Clemens 42449*, staminate plant). h, *L. glauca*, axillary cluster (*Gunn s.n.*, staminate plant). i, *L. banksii*, terminal cluster (*Brass 18849*, pistillate plant). (Filled crescents = cluster bracts; open crescents = bractlike structures; crosshatched crescents = outer whorl of tepals; filled circles = flowers; open circles = inflorescence axis; x = structure unclear.)

URE 3, o–w, especially o–r). In species of group A as a whole, the individual flowers are not completely ensheathed in bractlike structures, and the bracts are rather narrow and have acute tips. This contrasts with the often very broad, sheathing, innermost bractlike structures in section CEPHALOGYNE and in group B, below.

Species examined: *Lomandra bracteata* Lee, *L. brevis* Lee, *L. cylindrica* Lee, *L. densiflora* Black, *L. endlicheri* (F. Mueller) Ewart,[2] *L. effusa* (Lindley) Ewart, *L. fibrata* Black, *L. filiformis* (Thunb.) J. Britten, *L. micrantha* (Endl.) Ewart, *L. pauciflora* (R. Br.) Ewart, *L. preissii* (Endl.) Ewart,[2] *L. purpurea* (Endl.) Ewart,[2] *L. sororia* (F. Mueller) Ewart.

Group B. Species in this group have flowers in clusters grouped in whorls along the inflorescence axis. Prominent, pointed cluster bracts occur in many species, and in all species each flower is completely surrounded by bractlike structures, usually two or more in number (FIGURES 3, x; 4, a, b, f, g, i). Terminal clusters in *Lomandra longifolia*, *L. banksii*, etc., may lack cluster bracts, although these are associated with the clusters along the axis of the same inflorescence. The number of bractlike structures surrounding the flower may vary within a species (e.g., in *L. longifolia*).

Species examined: *Lomandra banksii* (R. Br.) Lauterbach, *L. dura* (F. Mueller) Ewart, *L. confertifolia* (F. M. Bailey) Fahn, *L. longifolia* Labill., *L. montana* (R. Br.) Fraser & Vickery, *L. multiflora* (R. Br.) J. Britten, *L. ordii* (F. Mueller) Ewart, *L. patens* A. Lee, *L. rigida* Labill., *L. spartea* (Endl.) Ewart, *L. spicata* A. Lee.

Summary of inflorescence variation in the Xeroteae. The inflorescences examined seem to belong to two types.

I. *Acanthocarpus* and *Lomandra papuana* have clearly cymose flower clusters, the single bract associated with each flower completely ensheathing both that flower and the younger part of the cluster. At least toward the base of the large and apparently complex inflorescence of *Lomandra macrostachya*, there are clearly cymose clusters of flowers; these clusters are borne on racemose side branches of a racemose main axis. This type of inflorescence, with cymose ultimate branch units borne on a racemose (monopodial) main axis, is common in monocotyledons (Tomlinson, 1970—see also diagrams in such books as Eichler, 1875; Stebbins (1974, p. 314) considers monocotyledons to have basically racemose or spicate inflorescences). It is also possible that the species of *Lomandra* in group A of section LOMANDRA have an inflorescence of a similar type, but much more reduced.

II. Those species in which each flower is surrounded by two or more bractlike structures (*Chamaexeros* and the rest of *Lomandra*) are not so easily related to an inflorescence with cymose clusters borne racemosely along an axis, although it is possible that each flower represents such a cymose cluster.

[2] Species with flower clusters in whorls.

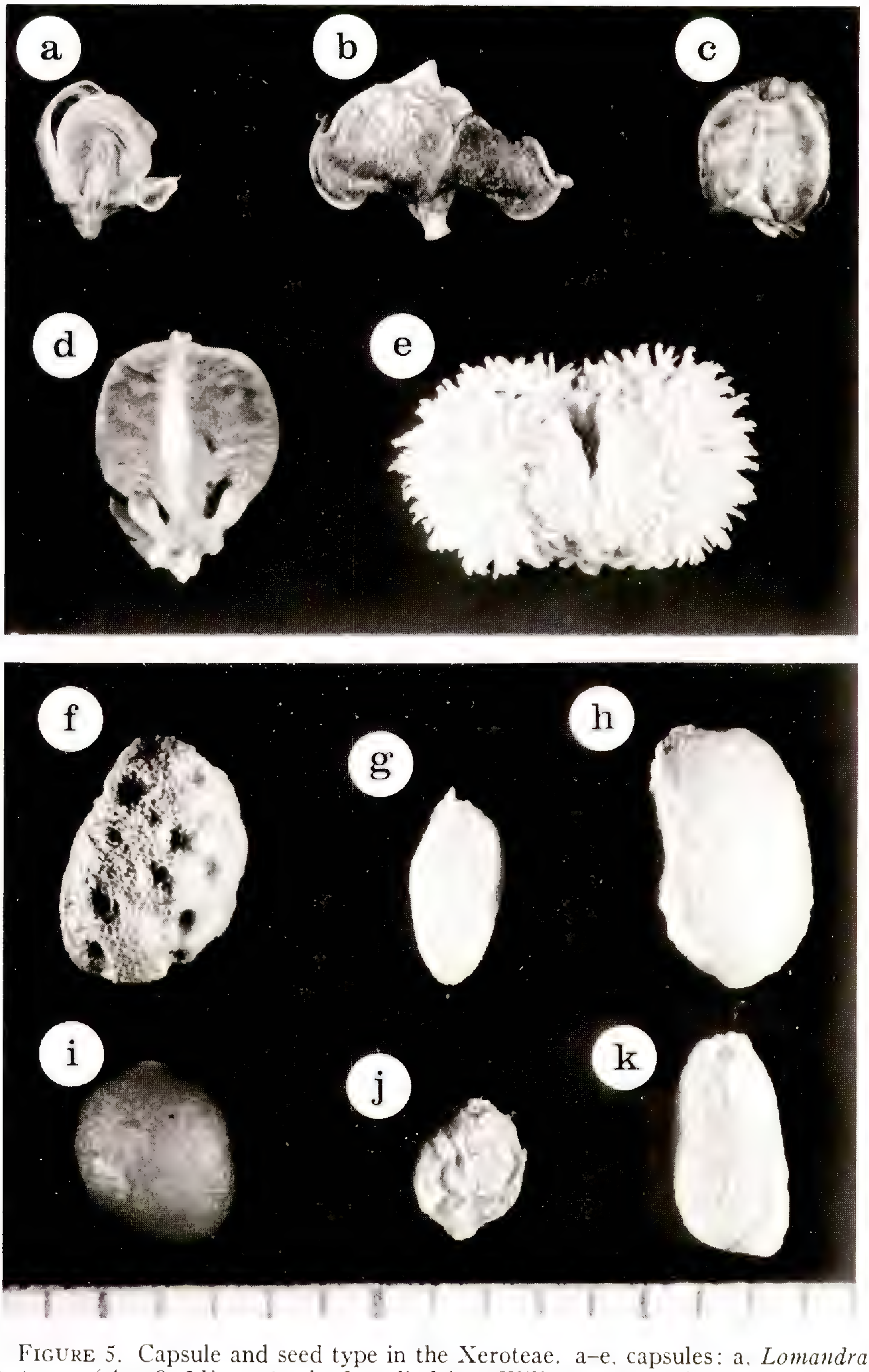

FIGURE 5. Capsule and seed type in the Xeroteae. a–e, capsules: a, *Lomandra papuana* (*Aet & Idjan 24*); b, *L. cylindrica* (*Wilkes s.n.*); c, *Chamaexeros fimbriata* (*Helms s.n.*, MEL 8378); d, *L. multiflora* (*Brass 18939*); e, *Acanthocarpus preissii* (*E. H. Wilson 300*). f–k, seeds: f, *L. papuana* (*Aet & Idjan 24*);

FLOWER TYPE. *Lomandra* has often been considered to be a genus of dioecious plants, but see Lee (1966). Perfect flowers, or flowers of the type other than that predominating on the plant, are to be found quite frequently in the otherwise staminate or pistillate inflorescences of some species (e.g., *L. bracteata*), and *L. hermaphrodita* was described from plants with perfect flowers, as its name implies. *Lomandra papuana*, *Acanthocarpus*, and *Chamaexeros* have flowers which appear to be perfect.

STIGMA AND STYLE. The stigma of *Lomandra* is characteristic, being prominently trifid with recurved lobes. The style is usually shorter than the ovary, although somewhat longer in species like *L. leucocephala*. *Lomandra papuana*, *Chamaexeros*, and *Acanthocarpus* have slender, usually long styles (but only about as long as the ovary in *L. papuana*) and very small stigmas which are not obviously 3-lobed.

OVULE POSITION. All species in the Xeroteae have 3-locular ovaries. The single, pendulous ovules of *Acanthocarpus* are borne near the top of the loculus. The paired ovules of *Lomandra papuana* are also clearly pendulous, and one is borne somewhat above the other. The ovules in *Chamaexeros* and *Lomandra* are less obviously pendulous; the paired ovules in the former genus are collateral.

FRUIT. The fruit of *Acanthocarpus* is densely covered by rather blunt spines (FIGURE 5, e); minute spines also occur near the top of the immature fruit of *Lomandra papuana*. The mature capsule of *L. papuana* is smooth (FIGURE 5, a), and in both species the young ovary is also smooth. All other taxa lack spines on both fruits and young ovaries, although the fruits may become more or less transversely wrinkled when ripe (FIGURE 5, b–d).

SEED SURFACE. *Lomandra papuana* has prominently foveate seeds, with pits penetrating the endosperm (FIGURE 5, f). The testa of a few other members of the Xeroteae may be irregularly wrinkled (FIGURE 5, g–k), but then the surface of the endosperm is smooth in all cases. *Acanthocarpus*, *Lomandra*, and *Chamaexeros* thus have similar seeds, but it should be noted that seeds of only twenty-two species of *Lomandra* and one species of *Chamaexeros* were examined (this species of *Chamaexeros*, *C. fimbriata*, is apparently the only species in the genus of which the seeds are known — Kuchel, 1976).

EMBRYO. The embryo of *Lomandra papuana* is vertical and central in position in the upper part of the seed, but then it becomes curved so that the micropyle is in the center of the outer part of the seed. In all other

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g, *L. cylindrica* (*Wilkes s.n.*); h, *L. multiflora* (*Brass 18939*); i, *A. preissii* (*E. H. Wilson 300*); j, *C. fimbriata* (*Helms s.n.*, MEL 8378); k. *L. longifolia* (*C. T. White 11612*). (Scale in millimeters.)

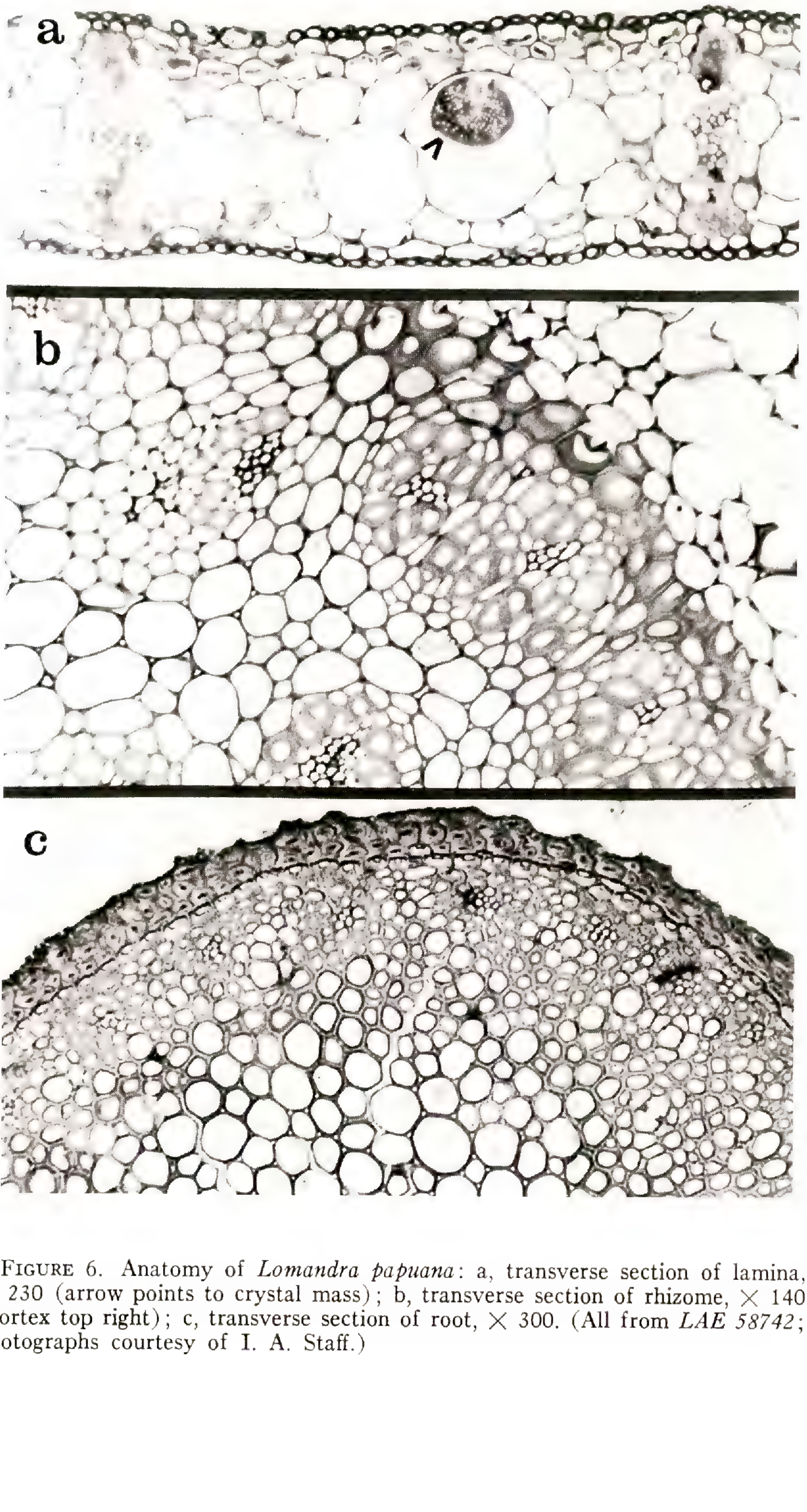


FIGURE 6. Anatomy of *Lomandra papuana*: a, transverse section of lamina, × 230 (arrow points to crystal mass); b, transverse section of rhizome, × 140 (cortex top right); c, transverse section of root, × 300. (All from *LAE 58742*; photographs courtesy of I. A. Staff.)

species of the Xeroteae in which seeds have been seen, the embryo is more or less straight for its whole length, the micropyle being near the base of the seed.

Anatomy. Dr. I. A. Staff (La Trobe University, Australia) examined the anatomy of the leaf blade and rhizome of *Lomandra papuana* (*LAE 58742*), and the description below is taken from notes that he sent. The specimens were swollen by heating in water, embedded in araldite resin, sectioned at about 2 μm., and observed with a Zeiss Standard Universal microscope.

Leaf (Figure 6, a). Thickness about 150 μm.; more or less isobilateral. Epidermal cells thick-walled, rounded. Stomata on both surfaces; guard cells and accessory cells thick-walled, the latter with a small beak bordering the pore. Hypodermis present. No clearly differentiated palisade mesophyll; the central mesophyll cells large and rounded, occasionally with a mass of crystals (birefringent in polarized light when viewed under crossed nichols) embedded in an amorphous matrix. Vascular bundle with ad- and abaxial sclerenchymatous girder extending to, but not including, the hypodermis; sheath cells noticeably smaller than the central mesophyll cells.

Rhizome (Figure 6, b). Epidermis of small, tightly packed, almost rectangular cells. Cortex parenchymatous. Endodermis with U-shaped thickenings. Vascular bundles most numerous just interior to the endodermis, amphivasal, although the xylem elements sometimes not completely surrounding the phloem. Ground parenchyma with numerous intercellular spaces. No secondary thickening observed.

Root (Figure 6, c). Mature root decorticates down to the innermost two layers of the cortex; these are heavily lignified and persistent. Endodermis heavily thickened on all walls except the outer tangential walls. Vascular tissue embedded in heavily lignified tissue close to the endodermis, with alternating areas of xylem and phloem. Pith of angular, isodiametric parenchymatous cells with numerous small intercellular spaces.

Summary of anatomical variation in the Xeroteae. From the information given by Fahn (1954) and confirmed by P. B. Tomlinson (pers. comm.), it seems that there are no major anatomical groupings recognizable within the Xeroteae; the Xeroteae themselves are separable from the other genera associated with them mainly in not having the characters that distinguish these other genera (see p. 131). Although cambium has been found in a number of species of *Lomandra* (Fahn, 1954; Staff, pers. comm.) and in *Acanthocarpus* (Tomlinson, pers. comm.), the taxonomic significance of its absence in *L. papuana* is unclear. The failure of the sclerenchymatous vascular bundle girders to reach the epidermis in *L. papuana* is uncommon in the Xeroteae, although it has been reported from *L. pauciflora* and *Chamaexeros* (Fahn, 1954). In other anatomical details *L. papuana* is similar to other Xeroteae.

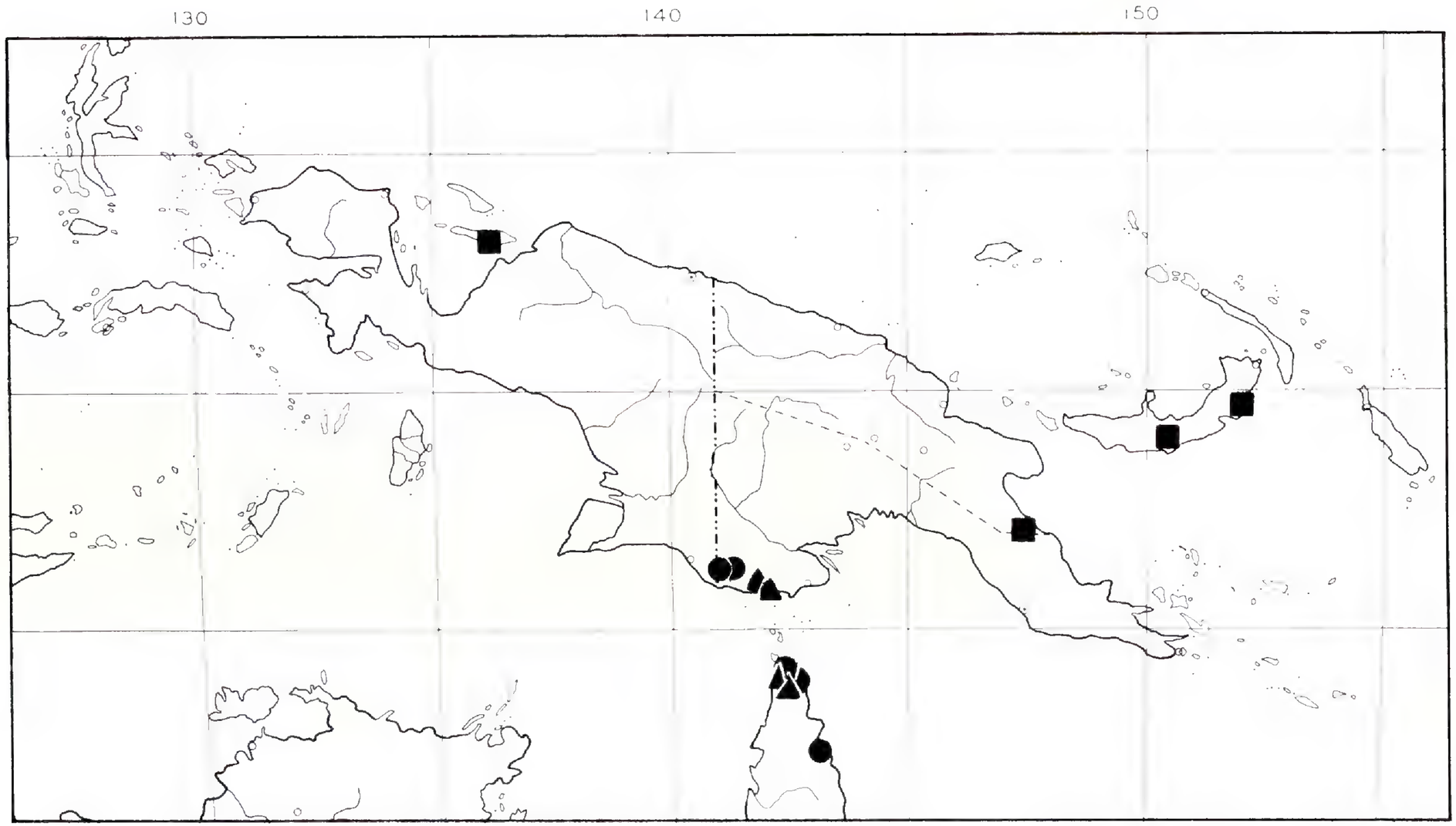
TAXONOMIC POSITION OF LOMANDRA PAPUANA

The relationships between *Lomandra papuana*, *Lomandra*, *Chamaexeros*, and *Acanthocarpus* appear to be reticulate (see especially TABLE 1). Each taxon can easily be distinguished from the others separately, but when one taxon is compared with the other three simultaneously, the distinction is less clear cut. All genera have a xeromorphic facies, and parallelism and superficial convergence obscuring taxonomic relationships in such plants are notorious.

Acanthocarpus and *Lomandra papuana* are similar in flower cluster structure, the spines or papillae on the (young) fruit, and the clearly pendulous ovules. *Acanthocarpus* can readily be separated from all other taxa in the Xeroteae by its fruit, which is spiny when mature, while *L. papuana* can be recognized by its foveate seeds and curved embryo. In facies the two are very different. *Acanthocarpus*, with its short, recurved leaves, long stem, and sessile inflorescence, approaches some members of *Lomandra* section CEPHALOGYNE (*L. mucronata* (R. Br.) A. Lee has been compared with *Acanthocarpus* (see Lee, 1972); Macbride (1918) considered it to be a species of that genus), although this growth form is uncommon in *Lomandra*. *Lomandra papuana*, with its long leaves serrate at the apex, its short stem, and its long, branched inflorescence, is similar to the majority of species of *Lomandra* in these respects.

Lomandra and *Chamaexeros* are similar in facies and inflorescence, and the diagnostic type of scarious leaf margin of the latter genus may be derived from a margin like that of some species of *Lomandra* (e.g., *L. sororia*). Variation in leaf type is comparable in the two genera: in *Chamaexeros* closely related species have either terete or flattened leaves, while in *Lomandra* there is infraspecific variation in leaf type; in both genera there are species with inverted vascular bundles in their leaves (Fahn, 1957). However, the stigma with three well-developed recurved arms which occurs in all species of *Lomandra* known to me is unique in the group; in stigma and style *Chamaexeros* approaches *L. papuana* and *Acanthocarpus*. *Chamaexeros* is usually considered to have a single ovule per loculus (see, for example, Bentham, 1878; Kuchel, 1976), but I have consistently found two ovules per loculus in all three species. All the pistillate or bisexual flowers of *Lomandra* dissected had but a single ovule per loculus.

The considerable variation in pollen type within *Lomandra* does not greatly aid the definition of generic boundaries. *Chamaexeros* (*C. serra*, *C. fimbriata*) and *Acanthocarpus* have similar boat-shaped, sulcate pollen grains, the sulcus dividing each grain into equal halves; there are no supra-tectal processes (Chanda & Ghosh, 1976). In twenty-four of the twenty-seven species of *Lomandra* that Chanda and Ghosh examined, the sulcate grains were either more or less spheroid, with supra-tectal processes, and divided by the sulcus into two equal halves, or disc-shaped, lacking processes, and divided by the sulcus into two unequal halves. However, three species, *L. micrantha*, *L. endlicheri*, and *L. leucocephala*,



MAP 1. Distribution of the Xeroteae in Papuasia and adjacent Queensland. Squares, *Romnalda papuana*; circles, *Lomandra multiflora*; triangles, *L. banksii*.

had spiraperturate or spiraperturate-type grains which Chanda and Ghosh (*op. cit.*) considered to be very different from the others. However, I know of no morphological or anatomical evidence to suggest that those three species should be placed in a genus other than *Lomandra*. (There was too little material of *L. papuana* for palynological examination in the current study.)

The variation pattern in the Xeroteae is best represented formally by recognizing four genera, *Lomandra papuana* being removed from *Lomandra* and becoming the type of the monotypic genus *Romnalda* (this generic name was chosen to emphasize the apparently reticulate nature of the relationships in the Xeroteae). *Chamaexeros*, *Lomandra*, and *Acanthocarpus* are maintained as genera; all three are natural taxa. It may be noted that if Ewart's (1916) reduction of *Chamaexeros* to *Acanthocarpus* is followed (see also Mueller, 1878; Engler, 1888), then there is no reason to keep either *Acanthocarpus* sensu lato or *Romnalda* separate from *Lomandra*, but then the resulting heterogeneity in the latter genus would not be taxonomically satisfactory.

Romnalda, from the tropical rainforests in the northern part of Papuasia (MAP 1), appears to be most closely related to *Acanthocarpus*, a genus growing in very much drier and more open conditions in sclerophyll vegetation in southwest Australia. *Romnalda* is clearly not immediately related to *Lomandra*, two species of which occur in relatively drier and open conditions in the Western Province of Papua New Guinea (MAP 1). The restriction of the Xeroteae within Malesia to the Papuasian region might be expected of such a xeromorphic, Australian-centered group, but there is clearly much work to be done before the rather puzzling relationships between members of this group are understood.

ARTIFICIAL KEY TO GENERA OF THE XEROTEAE

1. Plants usually dioecious; stigma of pistillate or the rare bisexual flowers with three prominent, recurved arms. ..... *Lomandra*.
1. Plants hermaphroditic; stigma minute, ± pin-shaped.
   2. Leaves with prominent scarious margins along their lengths (sometimes broken off in old leaves); each flower surrounded by a "bract plus bracteole." ..... *Chamaexeros*.
   2. Leaves lacking scarious margins except at their bases; each flower surrounded by only a single "bract."
      3. Inflorescence axes less than 3 mm. long; ripe capsules spiny; ovules one per loculus. ..... *Acanthocarpus*.
      3. Inflorescence axes 7–20 cm. long; ripe capsules smooth; ovules two per loculus. ..... *Romnalda*.

Romnalda P. F. Stevens, gen. nov.

A *Acanthocarpo*, *Lomandra* et *Chamaexeros* in seminibus foveatis et embryone curvato differt, a *Acanthocarpo*, quo aliter simile est, in loculis ovarii biovulatis, non uniovulatis, axe inflorescentiae elongato, non brevi, et capsula matura laevi, non echinata, a *Chamaexeros* in inflorescentia et

margine foliae, et a *Lomandra* in stylo stigmateque et numero ovularum differt.

Herba caule breve. Folia longa, apice serrata. Inflorescentia axe elongato; flores in cymulis densis aggregatis. Flos hermaphroditus; tepala tenacia, persistentia; stamina 6, antheris dorsifixis; ovarium 3-loculare, loculis ovulis duabus pendentibus plus minusve superpositis provisum; stylus longus; stigma parvum. Capsula loculicida 1–3-seminalis; semen foveatum, endospermio oleoso tenaci, embryone curvato, micropylo pagina extus inter medium basinque testae praesenti.

TYPUS (et species sola): *Romnalda papuana* (Lauterbach) P. F. Stevens.

THE PAPUASIAN XEROTEAE

Romnalda papuana (Lauterbach) P. F. Stevens, comb. nov.

Lomandra papuana Lauterbach, Bot. Jahrb. **50:** 294. 1913; Krause, Bot. Jahrb. **59:** 554. 1925. TYPE: [Papua New Guinea, Morobe Province] Goromia, 250 m., 8 March 1908, *Schlechter 17396* (holotype, B; isotype, WRSL).

Herb, stem prostrate or ascending, to 5 cm. long and 2–3 mm. thick. Leaves linear, apparently spirally arranged, congested, 22–38 cm. long and 4.4–5 mm. wide, acute at the apex, with 5 to 12 small teeth, pale dull green when dry, plane, nerves 12 to 15, margin and surface smooth, at the base widening gradually and with a somewhat scarious edge breaking irregularly and ± persisting as fibers. Inflorescence to 20 cm. long, sparsely and irregularly branched, with single clusters at the branching points and a few along the inflorescence, 1 to 3 together at the end, first cluster often only 1 cm. or so above the base; cluster consisting of a large cluster bract to 3 cm. long subtending numerous bracts plus flowers, each flower terminal, it and the younger part of the cluster ensheathed by a bract; pedicel flattened, 3.2–4 mm. long. Flower apparently hermaphroditic; tepals 6, the outer three ovate, greenish, ca. 3.5 mm. long and 1 mm. wide, the inner tepals white, ± elliptic, ca. 3.75 mm. long and 0.75 mm. wide; stamens 6, the filaments connate for the basal 0.5 mm., flattened, narrowly triangular, filaments of stamens opposite the outer whorl of tepals ca. 2.2 mm. long, ± adnate to the tepals for the basal 0.5 mm., filaments of stamens opposite the inner whorl of tepals ca. 2.5 mm. long, adnate to the tepals for the basal 0.7–1 mm., the anthers ca. 1 mm. long, dorsifixed, dehiscence latrorse; ovary ± ovoid, smooth, ca. 1.5 mm. long, 3-locular, ovules 2 per loculus, pendulous, ± superposed; style ca. 1 mm. long; stigma small, capitate. Fruit a loculicidal capsule, surrounded by the persistent tepals at the base, green, usually asymmetrically ovoid, 4–4.7 mm. long and ca. 3.7 mm. across, pointed at the apex, smooth when mature, minutely spiny when young; seeds 1(to 3), slightly flattened-ellipsoidal, brownish, ca. 4.7 mm. long, 3.8 mm. wide and 3 mm. deep, foveate, the testa finely reticulate, the embryo curved, the micropyle facing outward.

DISTRIBUTION. Papuasia, scattered in the northern part (MAP 1).

ADDITIONAL SPECIMENS SEEN. **Papuasia.** IRIAN JAYA. Geelvink Bay: Jappen-Biak, Saroerai near Seroei, *Aet & Idjan* (exp. L. J. van Dijk) *24* (A, K, L). PAPUA NEW GUINEA. New Britain: Mt. Klangal, 40 km. N.N.E. of Gasmata, Kandrian subdistrict, West New Britain, 800 m., *NGF 41283* (A, B, LAE); mapping site at edge of Mengen Massif, Pomio subdistrict, East New Britain, 960 m., *LAE 58742* (A, B, LAE).

ECOLOGY. *Romnalda papuana* is a very locally abundant plant of colline rain forest, growing from 250 to 960 meters altitude. The collections from New Britain were made in forest with much *Castanopsis acuminatissima*, in a creek (*NGF 41283*) or on a dry, stony ridge (*LAE 58742*).

On New Britain *Romnalda papuana* was growing in the same area as a species of *Alpinia* section MYRIOCRATER, which also has long-lived inflorescences.

KEY TO THE PAPUASIAN SPECIES OF LOMANDRA

1. Shrublet to 2 m. tall; leaves dehiscing just above the base, the part remaining becoming recurved and persisting. ..... *L. banksii.*
1. Herb, stem a short underground rhizome; leaves not dehiscing above the base, but the whole leaf gradually withering. ..... *L. multiflora.*

F. von Mueller was the first to record *Lomandra* from Papuasia (Mueller, 1876; as *Xerotes banksii*). This record was based on a sterile specimen collected by J. Orkney (properly Orknie) near the Baxter River (the Mai Kussa, in the Western Province of Papua New Guinea). Lauterbach (1913) and Krause (1925) repeated this report, but it was not until the 1936–37 Archbold Expedition that the species was re-collected by L. J. Brass. In 1966 a second species, here identified as *L. multiflora*, was collected from the Western Province.

Lauterbach (1913) recorded *Lomandra longifolia* Labill. from Java, but *Lomandra* is not included by Backer and Bakhuisen f. (1968) in their *Flora of Java* and is probably not native there. The two species of *Lomandra* from Papuasia appear to be the only two at present known from Malesia.

Lomandra banksii (R. Br.) Lauterb. Bot. Jahrb. **50**: 294. 1913; Krause, Bot. Jahrb. **59**: 554. 1925; *Xerotes banksii* R. Br. Prodr. 1: 263. 1810; F. Mueller, Descr. Notes Papuan Pl. 1. 3: 45. 1876. TYPE: Australia, Queensland, Endeavour River, *Banks & Solander* anno 1770 (holotype, BM).

Undershrub to 2 m. tall; stem 6–7.5 mm. across. Leaves distichous, rather scattered, linear, 25–40 cm. long and 3.5–4.7 mm. across, with (1 to)3 obscure teeth at the apex, pale dull green when dry, plane, nerves 33 to 45, margin minutely scaberulous, broadening somewhat toward the base, at the base with a subpersistent scarious margin splitting irregularly, ca. 0.5 cm. of the leaf persisting and becoming strongly recurved after

the rest abscises. Plants dioecious: staminate and pistillate inflorescences similar, apparently terminal (growth of the stem continued by an axillary bud developed just below the inflorescence), paniculate, once or twice branched, smooth, lowest whorl of branches borne 5–15 cm. above the base, usually at least 2 cm. between whorls, branches to 12 cm. long, perhaps rather shorter in pistillate than in staminate plants. Staminate plants: flower clusters along the stem each subtended by a cluster bract to 1 cm. long, 1- to 7-flowered, the terminal clusters 10- to 20-flowered, apparently lacking cluster bracts; flowers sessile, each ensheathed by two further bractlike structures up to 1 mm. tall; tepals 6, free, the outer three tepals ovate, 2.2–2.5 mm. long and ca. 1.5 mm. wide, the inner three tepals ovate, ca. 3 mm. long and 1 mm. wide; stamens 6, the filaments flattened, filaments of stamens opposite the outer whorl of tepals ca. 1.7 mm. long, adnate to the tepals for ca. 0.5 mm., filaments of stamens opposite the inner whorl of tepals ca. 2.1 mm. long, adnate to the tepals for ca. 1.5 mm., the anthers ca. 0.5 mm. long, dorsifixed, dehiscence latrorse; pistillode prominent, ca. 1.5 mm. long, stigmas not developed. Pistillate plant: flower clusters along the stem each subtended by a thick cluster bract ca. 5 mm. long, 1- to 3-flowered, terminal clusters 5- to 8-flowered, outer flowers subtended by "cluster bracts," inner flowers lacking them; flowers sessile, usually with a single additional ensheathing bractlike structure, sometimes with two; tepals free, the outer tepals ovate, 4.3–4.5 mm. long and ca. 3.2 mm. across, the inner tepals ± triangular, 4.6–4.8 mm. long and ca. 2.8 mm. across, margins incurved; stamens very much as in staminate flowers, but anthers rudimentary; ovary ovoid, 3-angled, ca. 2.7 mm. long and 1.9 mm. across, 3-locular, one ovule per loculus, ovary continuous with the style; style ca. 1.3 mm. long, with three longitudinal ridges; stigma papillate, with three short, retrorse arms. Fruit a loculicidal capsule, surrounded by persistent tepals at the base, ovoid, 8–9 mm. long and 5–7 mm. across, usually 3-seeded, strongly pointed at the apex, the valves with 4 to 5 fine transverse wrinkles per 1 mm.; seeds ellipsoid, slightly curved or not, orange when dry, ca. 5 mm. long and 3–3.5 mm. across, the testa coarsely and irregularly reticulate, the embryo almost straight, the micropyle basal.

DISTRIBUTION. Papua New Guinea, the Western Province, and Australia (Queensland) (MAP 1); ?New Caledonia.

SPECIMEN FROM PAPUASIA EXAMINED: **Papua New Guinea (Papua). WESTERN:** Tarara, Wassi Kussa River, *Brass 8700* (pistillate and carpellate plants: A).

ECOLOGY. *Lomandra banksii* is reported as being an occasional subshrub in dense savannah forests at low altitudes. It was in flower and young fruit when collected in January.

The description of the fruit and seed was taken from *Brass 18512*, collected in the Cape York Peninsula, Queensland, Australia. Agreement between Australian and Papuasian specimens is excellent, and they grow in similar habitats. The staminate inflorescences of *Brass 8700* tend to have alternate, rather than whorled, branching, but this is probably an

abnormality, part of one inflorescence being weakly fasciated. The reports of *Lomandra banksii* from New Caledonia (e.g., Mueller, 1876) should be re-examined.

Lauterbach (*loc. cit.*) was the first to transfer *Xerotes banksii* to *Lomandra*, making the combination three years before Macbride (1916), who is usually given as the author of the combination.

Lomandra multiflora (R. Br.) J. Britten in Banks & Solander, Ill. Bot. Cook's Voy. 3: 95. *pl. 313*. 1905; *Xerotes multiflora* R. Br. Prodr. 1: 262. 1810. TYPE: Australia, *Banks & Solander s.n.* (n.v.).

?Lomandra Ridsdale, Papua New Guinea Sci. Soc. Trans. 8: 22. 1969.

Rhizomatous herb, the rhizome near the surface of the ground, ca. 3 mm. across. Leaves ± distichous, aggregated, linear, up to 72 cm. long and (0.6–)2.5–4 cm. across, rounded to obtuse at the apex, when alive yellowish green, when dry dull greenish brown, inrolled, the nerves (7 to) 15 to 21, the surfaces and margins of the leaf minutely scaberulous, at the base gradually expanded, the margins dark brown, ± scarious, splitting irregularly and not persistent. Plants dioecious. Staminate inflorescence: 50–65 cm. long, scaberulous, especially toward the apex, twice branched the branches whorled, 2–5.5 cm. between the whorls, the lowest whorl 20–30 cm. from the base of the inflorescence, with 6 to 12 branches, the bracts subtending the branches 2–10 mm. long, the branches to 11 cm. long; clusters of flowers borne in whorls of 3 toward the apex of the branches, the cluster bracts to 3 mm. long, the terminal cluster surrounded by ca. 3 cluster bracts; flowers 2 to 4 per cluster, each flower surrounded by 2, very rarely 3, "bracts," the pedicels up to 1 mm. long; flowers greenish yellow; tepals ovate, 6, almost free, the outer three tepals ca. 1 mm. long and 0.7–0.8 mm. across, the inner three tepals ca. 0.8 mm. long and 0.5 mm. across, thicker; stamens 6, the filaments adnate to the tepals for ca. 0.2 mm., the free part of the filaments opposite the outer whorl of tepals very short, that of the filaments opposite the inner whorl up to 0.1 mm. long, the anthers oblong, 0.35–0.45 mm. long, dorsifixed; pistillode minute. Pistillate inflorescence: 28–30 cm. long, scaberulous, unbranched; clusters of flowers in whorls of up to 6, 1–2.5 cm. distant, the cluster bracts to 7.5 mm. long; flowers 2 to 6 per cluster, "bracts" apparently as in staminate flowers; pedicels absent; tepals ovate (persisting at the base of the fruit), the three outer ca. 3.1 mm. long and 2.9 mm. across, the three inner ca. 2.5 mm. long and 1.5 mm. across; ovary and staminodes unknown, but fruit crowned by three persistent, recurved stigmatic lobes. Fruit a loculicidal capsule, at maturity generally with a single seed, asymmetrical, 6–6.5 mm. long, 3.3–4 mm. across and ca. 5 mm. deep, grayish brown when dry (the sutures brown), with distant transverse wrinkles; seeds slightly curved, ellipsoid, 5.5–6 mm. long, 3.3–4 mm. across and 3–3.5 mm. deep, the testa minutely reticulated, the anticlinal cell walls being prominent, the embryo slightly curved, the micropyle basal.

DISTRIBUTION. Papua New Guinea, the Western Province (MAP 1); widespread in Australia.

SPECIMENS FROM PAPUASIA EXAMINED. **Papua New Guinea (Papua).** WESTERN: near Weam, 30 m., *NGF 33573* (staminate: CANB, K, LAE), *NGF 33574* (pistillate: A, CANB, K, LAE); ca. 5 km. W. of Morehead River at lat. 8° 48′ S., 15 m., *Paijmans 304* (staminate: CANB).

ECOLOGY. *Lomandra multiflora* grows in open savannah; specimens with both flowers and fruits have been collected in August.

Although *Lomandra multiflora* is a very variable species, the specimens described above at first sight look completely different from the common form of the species. This latter has a smooth inflorescence axis, pedicels up to 10 mm. or more long, and staminate flowers over 2 mm. long. However, small-flowered specimens from Queensland (e.g., *Brass 18939*, Cape York Peninsula) have pedicels about 3 mm. long, and other specimens with larger flowers may have scaberulous inflorescence axes. Hence the broad circumscription of *L. multiflora* adopted by Bentham (1878) and Lee (1966) is followed.

The description above is taken entirely from the Papuasian specimens.

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RHIZOPHORA IN AUSTRALASIA — SOME CLARIFICATION OF TAXONOMY AND DISTRIBUTION

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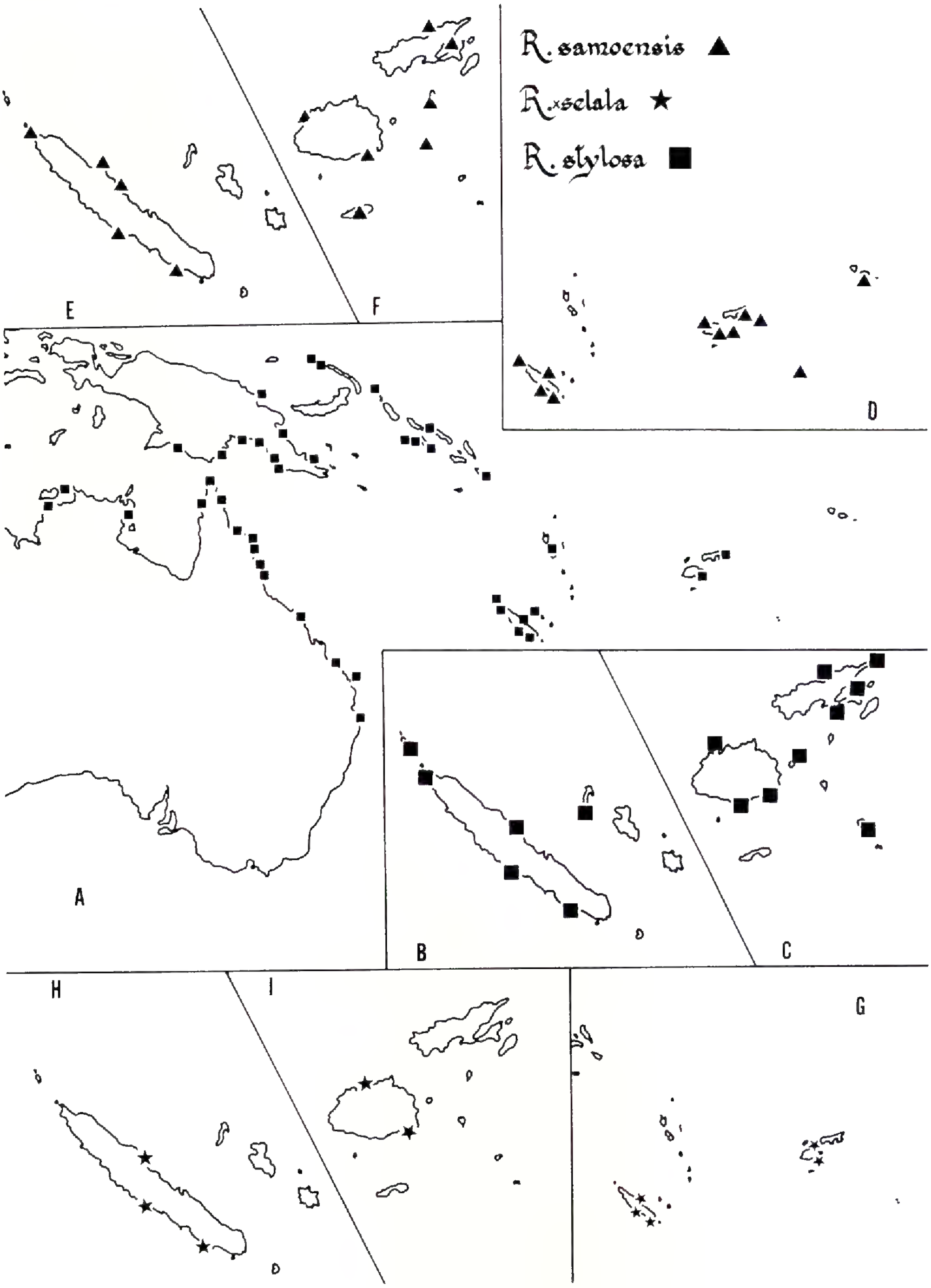
THE WESTERN PACIFIC is known as an area of floristic discontinuity where many species with a wide distribution in the Indo-Malayan region terminate their range (Thorne, 1969). Consequently, precision is required in mapping plant distribution in this area. The important pantropical genus *Rhizophora* is an example of particular interest because it has long been recognized (Salvoza, 1936; Ding Hou, 1960) that in the western Pacific there is an area of overlap between the group of four taxa with an "Indo-Pacific" distribution (i.e., *R. apiculata* Bl., *R.* × *lamarckii*[1] Montr., *R. mucronata* Lamk., *R. stylosa* Griff.) and the three species with an "Atlantic" distribution (*R. harrisonii* Leechman, *R. mangle* L., *R. racemosa* G. F. W. Meyer). The overlap is occasioned by the extension of the range of the Atlantic species into the western Pacific via a form of *Rhizophora mangle* sufficiently distinct to be recognized and named as either a variety (var. *samoensis* Hochr.) or even a separate species (*R. samoensis* (Hochr.) Salvoza). A consequence of this overlap is the production of hybrid populations in the form of a taxon here recognized as *R.* × *selala*. Problems have arisen because the diagnostic features which are clear in the field (although small) are often obscured in herbarium specimens, resulting in frequent misidentification of dried material. Also, the area falls outside that covered by *Flora Malesiana*, so the account by Ding Hou (1958) of the genus in Malesia does not provide details of distribution in the area considered here.

Recent field work in this area, partly summarized here, now allows further precision to be brought to generalized statements and confirms earlier evidence of hybridization (Guppy, 1906; Tomlinson & Womersley, 1976) which is of phytogeographic and evolutionary interest. Direct observation of wild populations in several countries has been supplemented by study of herbarium materials at A, BRIS, GH, K, SUVA, NOU. Measurements reported later were all made on fresh or fluid-preserved specimens.

Since New Caledonia is one of the areas visited, and as it is particularly rich in *Rhizophora* species, some of which have been confused in earlier accounts, this island has been given special consideration. One taxon new to its flora, *R.* × *selala*, is recognized here. Fiji is also considered in some detail. My present understanding of the distribution of these taxa is summarized in MAPS 1–3.

[1] The name *Rhizophora* × *lamarckii* (Montr., Mém. Acad. Sci. Lyon **10**: 201. 1860, *pro sp.*) indicates the hybrid status of this entity (Tomlinson & Womersley, 1976).



MAP 1. Distribution of **Rhizophora** in Australasia. A–C, *R. stylosa*: A, generalized distribution in the southeastern part of its range; B, details of distribution in New Caledonia; C, details of distribution in Fiji. D–F, *R. samoensis*: D, distribution in the south-central Pacific (New Caledonia to Samoa); E, details of distribution in New Caledonia; F, details of distribution in Fiji. G–I, *R.* × *selala*: G, total known distribution; H, distribution in New Caledonia; I, distribution in Fiji. (Most localities refer to herbarium specimens seen by the author, but supplemented by field observations in Fiji, New Caledonia, Queensland, and New Guinea.)

TYPIFICATION AND DISTRIBUTION OF RHIZOPHORA × SELALA

Guppy (1906) described and illustrated a form of *Rhizophora* in Fiji which was characterized by the absence of fruits and, consequently, of viviparous seedlings. He used the name "Selala" to refer to this plant, from the native name signifying empty ("lala") flowers ("se"), but did not validly describe it. He considered it likely that this entity was a hybrid between the two fertile species he recognized in Fiji (which he called *R. mucronata* and *R. mangle*). More recent work supports this interpretation, although with changes in Guppy's nomenclature. On the basis of Guppy's descriptions, Salvoza (1936) used the name *R. mucronata* var. *selala*. This is unfortunate because Guppy's use of the name *mucronata* is incorrect. Modern work shows that he confused *R. stylosa* and *R. mucronata*. It seems certain that *R. mucronata* does not occur in Fiji (cf. Richmond & Ackermann, 1975), and that the one parent of the hybrid is actually *R. stylosa*. The other parent may be referred to most conveniently as *R. samoensis*. Guppy discussed the difference between Fijian and American populations of *R. mangle* and concluded that they were morphologically distinct. This is supported by the present work,

FIGURE 1. Floral features and diagnostic details of **Rhizophora × selala.** A–C, just-opened flower, × 2: A, side view; B, median longitudinal section; C, from above. D–F, floral details, × 2: D, style; E, dehisced stamen; F, petal. G, H, inflorescences, × ⅓: G, 5-flowered; H, 4-flowered and with regular dichotomy. I, floral diagram; J, diagram to show one type of inflorescence branching. (All drawn from *P. B. Tomlinson & T. Richmond 18.XI.74 A*, from Kinoya, Viti Levu, Fiji.)

and the name *R. samoensis* provided by Salvoza (1936) recognizes this distinction. In contrast, neither Ding Hou (1960) nor Breteler (1977), on the basis of herbarium studies, considers the small differences between the two forms sufficient to merit segregation of *R. samoensis* from *R. mangle*. The further problem of *Rhizophora* in Pacific America can only be solved by extensive field work and the establishment of further diagnostic differences, which is not within the scope of the present account.

Most recently, *R.* × *selala* has been shown to occur abundantly in New Caledonia. This suggests that the name used by Guppy should be given formal recognition.

Rhizophora × **selala** (Salvoza) Tomlinson, comb. et stat. nov.

FIGURE 1.

"*Selala*" Guppy, Obs. Nat. Pacific **2:** 445, 487. *frontisp.* 1906.
Rhizophora mucronata Lamk. var. *selala* Salvoza in Bull. Nat. Appl. Sci. Univ. Philip. **5:** 219. 1936.
Rhizophora 'selala' Tomlinson & Womersley in Contr. Herb. Austral. **19:** 9. 1976. *Nomen illegit.*

A *Rhizophora mangle* differt: foliis mucronatis mucrone demum recurvato (FIGURE 4); axe inflorescentiae crassiore longiore et floribus (2–9) plus quam *R. mangle* (2–6) praedito; gemmis maturis albis ad 14 mm. longis, pedicellum versus angustatis, in sectione transversali rotundis; bracteola manifesta sub flore omni; ovario apice conico in stylum ca. 1 mm. longum producto.

TYPE. *Frontispiece* (and p. 445). "Selala, Vanua Levu, Fiji," *Guppy*. 1906.

OTHER COLLECTIONS. **Fiji:** Kinoya Village, near Suva, Viti Levu, *P. B. Tomlinson & T. Richmond 18.XI.74 A* (A). **New Caledonia:** common in association with its putative parents in mangrove swamps on both coasts (e.g., Teremba, *P. Morat, J.-M. Veillon, & P. B. Tomlinson 18.VII.77 B* (A, NOU); Poindimié, *P. Morat, J.-M. Veillon, & P. B. Tomlinson 19.VII.77 C* (A, NOU).

This species differs from *Rhizophora samoensis* in having a leaf apex with an appreciable but ephemeral mucro, which becomes recurved with age (FIGURE 4). The inflorescence axis (FIGURE 1, G, H) is longer, thicker, and often with more flowers (2 to 9, sometimes more). The flower buds at maturity are white (not yellow), rounded (not angular) in cross section, up to 14 mm. long, and gradually (not abruptly) narrowed to the pedicel. The bracteole below the flower is distinct (2–3 mm. long) and not obscure as in *R. samoensis*. The top of the ovary is conical, with a distinct style scarcely 2 mm. long (FIGURE 1, D), i.e., shorter than in *R. stylosa* (FIGURE 3, C) but longer than in *R. samoensis*, which has a steeply conical ovary (FIGURE 2, E). Populations of *R.* × *selala* in New Caledonia and Fiji seem indistinguishable.

With fresh material of mixed populations at hand, it is easy to allocate a given specimen to one of the three species; to provide comparative in-

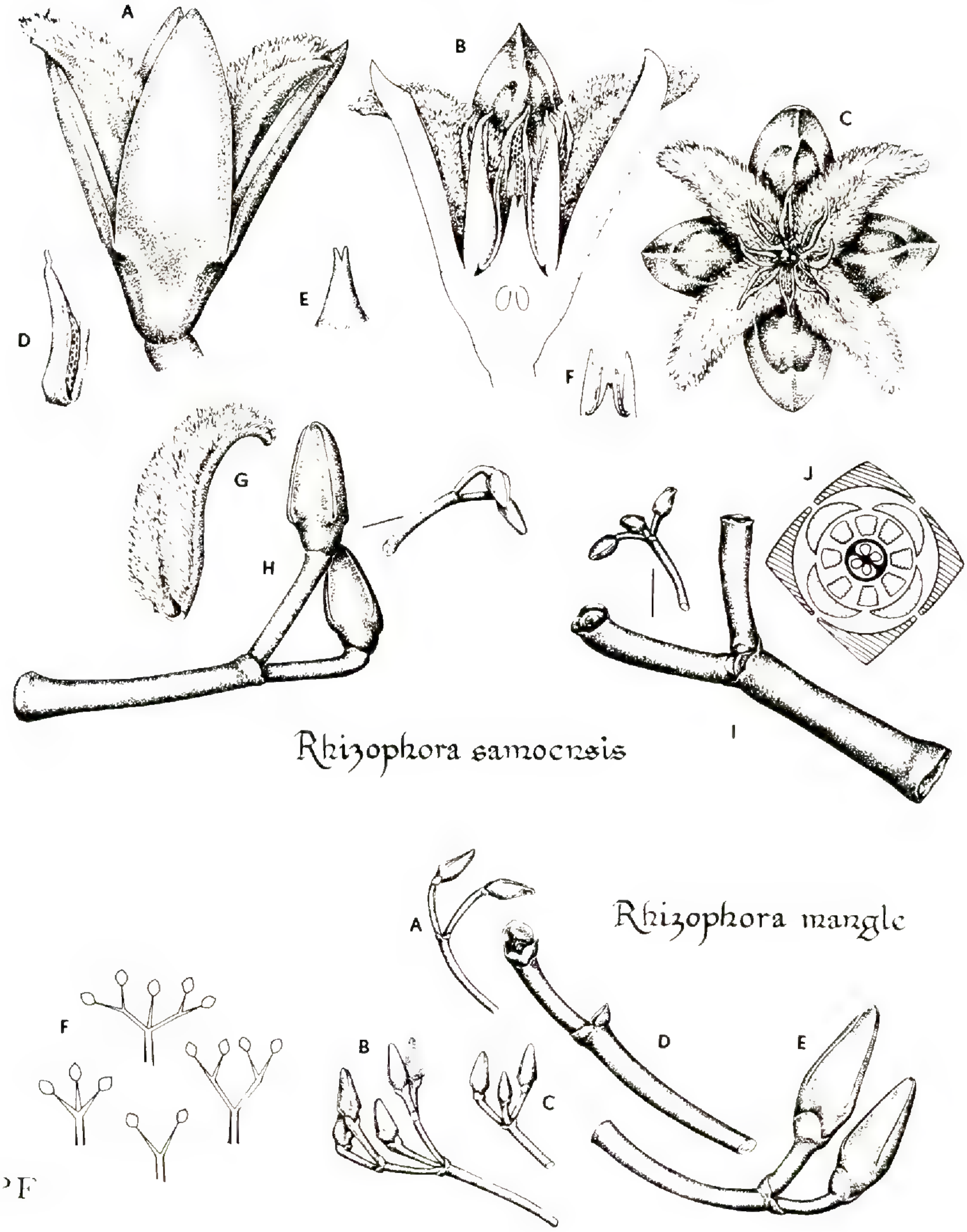


FIGURE 2. Comparison of **Rhizophora samoensis** and **R. mangle.** Above: *Rhizophora samoensis.* A–C, just-opened flower, × 2: A, side view; B, median longitudinal section; C, from above. D–G, details of flowers: D, dehisced stamen, × 2; E, style, × 2; F, relation between style and dehisced stamens, in median longitudinal view; G, petal, × 2. H, 2-flowered inflorescence, × 1 and × ⅓. I, 3-flowered inflorescence at the same magnifications; flowers removed in larger figure to show obscure bracteoles. J, floral diagram. (All drawn from *P. B. Tomlinson & T. Richmond 18.XI.74 C*, from Queen Elizabeth Drive, Suva, Viti Levu, Fiji.) Below: *Rhizophora mangle*, details of inflorescence to show diagnostic features. A–C, 2-, 5-, and 3-flowered inflorescences, respectively, all × ⅓. D, E, details of 2 inflorescences, × 1, showing obvious bracteoles. F, examples of typical branching patterns of inflorescence, often with trifurcation at first node. (All drawn from *P. B. Tomlinson s.n.*, Fairchild Tropical Garden, Miami, Florida.)

formation, a series of illustrations emphasizing certain diagnostic features is included in FIGURES 1–3. Apart from the morphology of the leaf tip (FIGURE 4), *R.* × *selala* also can be recognized because it often has a trichotomy of the first node of the inflorescence, whereas branching in *R. stylosa* is exclusively dichotomous. Flower buds in *R.* × *selala* are white rather than yellow as in *R. samoensis*. In addition, illustrations of *Rhizophora mangle* from South Florida show how it differs from *R. samoensis* in its conspicuous bracteoles (FIGURE 2).

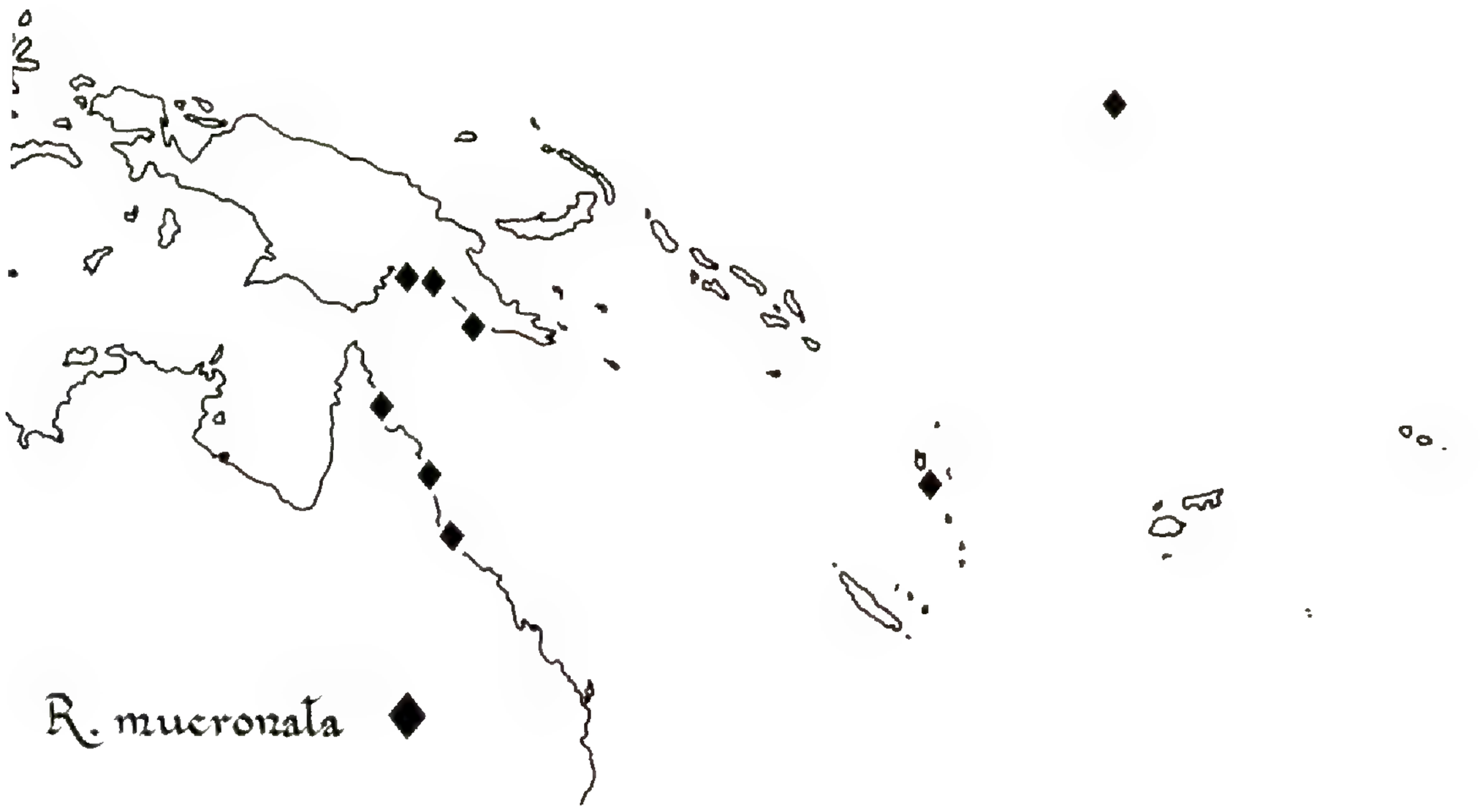
Guppy (1906) referred to two forms of *Rhizophora* × *selala*, the second distinguished from the one described above by its larger numbers of flowers (up to 24) because the inflorescence is branched 4 to 5 times. I have not seen this second form.

RHIZOPHORA IN AUSTRALASIA

With the above clarification, it now becomes possible to provide a diagnostic key to *Rhizophora* species in this area of overlap in the western

FIGURE 3. **Rhizophora stylosa,** habit and diagnostic features. A, leafy shoot with axillary inflorescence, × ⅓; inset, leaf apex. B, same with leaf blades removed to show extensively branched inflorescence. C, style, × 3. D, constructional principle of inflorescence. (All drawn from *P. B. Tomlinson 30.X.74 C*, from Bootless Bay, Port Moresby, Papua New Guinea.)

Pacific. Distributional information summarized in the key is shown in detail in MAPS 1–3. These are drawn up from limited sampling of herbarium material together with field study. Undoubtedly, the range of species needs to be expressed with further precision in the future, but the present summaries are more accurate than the generalized map of Ding Hou (1960). In the following key, measurements represent approximate values and may be exceeded in individual specimens. Only *Rhizophora stylosa*, *R. samoensis*, and *R.* × *selala* are illustrated; detailed drawings of *R. apiculata* and *R.* × *lamarckii* are given in Tomlinson and Womersley (1976).



MAP 2. **Rhizophora mucronata.** Distribution in Australasia (continued), based on herbarium specimens seen by the author. Its absence from New Caledonia and Fiji is supported by field observation. It is likely to occur in the Bismarck Archipelago and the Solomon Islands.

KEY TO RHIZOPHORA IN AUSTRALASIA

1a. Apex of leaf with a persistent extended mucro 2–3 mm. long (e.g., FIGURE 4, D–F); leaf blade usually 10–20 cm. long; inflorescence branching exclusively by dichotomy (e.g., FIGURE 3, B, D), never trifurcated, peduncle scarcely flattened. Flowers never in 3's. Mature flower buds white or greenish yellow (never yellow), 15 mm. or more long, rounded in cross section, pedicel of individual flowers often short or obscure. Stamens 8, 12, or 16; petals glabrous or hairy. ("Indo-Malayan group"; species group ranging from East Africa to the Western Pacific.) 2.

1b. Apex of leaf without a prominent apical mucro (e.g., FIGURE 4, A–C, G–M); leaf blade usually <10 cm. long. Inflorescence axis flattened and frequently trifurcated at the first (rarely subsequent) nodes. Peduncle often flattened. Flowers commonly in 3's. Mature flower bud white or yellow, somewhat angular in cross section, <15 mm. long. Pedicel of individual flowers always distinct. Stamens 8; petals always

woolly-hairy. ("Atlantic group"; species group ranging from New Caledonia to West Africa.) ..... 5.

2a. Stamens 8; petals conspicuously woolly-hairy on the margins. Leaf blade usually less than 15 (to as short as 8) cm. long. Mature flower buds white, ca. 15 mm. long. Inflorescence long-stalked, peduncle usually longer than 2.0 cm., usually branched to more than 2 orders. Flowers usually more than 4 per inflorescence; pedicel evident.

3a. Apex of ovary extended abruptly into a style ca. 3 mm. long. (Common and widely ranging throughout the South Pacific to Samoa and Tonga (MAP 1, A–C).) ..... *Rhizophora stylosa* (FIGURE 3).

3b. Apex of ovary bluntly conical, lacking a distinct style. (Extending into the South Pacific as far as the New Hebrides, apparently absent from New Caledonia and Fiji (MAP 2).) ..... *Rhizophora mucronata*.

2b. Stamens most commonly either 12 or about 16; petals glabrous or with inconspicuous marginal hairs. Leaf blade commonly 15 cm. long (sometimes more). Flower buds greenish yellow, never white, 15–20 mm. long at maturity. Inflorescence short-stalked, peduncle 1–2 cm. long, never branched to more than 2 orders. Flowers 2 to 4 per inflorescence; pedicel short and more or less obscured by bracteoles. ..... 4.

4a. Stamens usually 12, petals glabrous. Flowers usually 2 per inflorescence, peduncle short (usually <1 cm.). Inflorescence developing slowly and at maturity borne below the leafy crown. Bracts and bracteoles thick, rough, corky. Style absent. Plants fertile, with corky fruits and viviparous seedlings on the older parts of the twigs. (Common and wide ranging, but not further east than the New Hebrides; in New Caledonia restricted to the northeast coast (MAP 3, A, B).) ..... *Rhizophora apiculata*.

4b. Stamens varying in number, but based on 16; petals sparsely hairy on the margins. Flowers usually 4 per inflorescence, peduncle moderately long (1–2.5 cm.). Inflorescence borne within the leafy crown. Bracts and bracteoles not corky. Style distinct. Plants sterile, virtually lacking fruits and viviparous seedlings. (Scattered in Papuasia (MAP 3, C); always in association with its putative parents, e.g., in New Caledonia restricted with *R. apiculata* to the northeast coast (MAP 3, D).) ..... *Rhizophora* × *lamarckii*.
(A probable F_1 hybrid, *R. stylosa* × *apiculata*; Tomlinson & Womersley, 1976.)

5a. Leaf apex blunt, recurved (FIGURE 4, A–C). Peduncle 2–2.5 cm. long or longer, 2–2.4 mm. in diameter, uncommonly branching beyond 2 orders. Flowers usually 2 to 5 per inflorescence. Bracteoles scarcely developed and represented by a narrow rim of tissue (FIGURE 2, H–I). Mature flower buds yellow, angular in cross section and with a distinct basal shoulder, i.e., abruptly narrowed below, 10–12 mm. long at maturity. Apex of ovary steeply conical and without a distinct style. Plants fertile, with fruits and viviparous seedlings (FIGURE 2). (Apparently restricted to New Caledonia, Fiji, Samoa, and Tonga (MAP 1, D–F); its status in South America is disputed (cf. Breteler, 1977). *Rhizophora mangle*, apart from its distribution in West Africa and Tropical America, is distinguished by its conspicuous bracteoles and pointed flower buds, as shown in FIGURE 2.) ..... *Rhizophora samoensis*.

5b. Leaf apex initially with an indistinct but usually soon deciduous or recurved mucro (FIGURE 4, H–M). Peduncle 2.5–3.0 cm. long but often

longer, 2.6–3.2 mm. wide, commonly branched beyond 2 orders. Flowers 2 to 9 per inflorescence. Bracteoles distinct, ca. 1 mm. long. Mature flower buds white, neither sharply angular in cross section nor abruptly narrowed to a distinct shoulder at the base, 12–14 mm. long. Apex of ovary extended into a distinct style 1–2 mm. long. Plants sterile, lacking fruits and viviparous seedlings. (Presently known from Fiji and New Caledonia; always in association with its putative parents (MAP 1, G–I).) ..... *Rhizophora* × *selala*.

(A probable F_1 hybrid, *R. stylosa* × *R. samoensis*.)

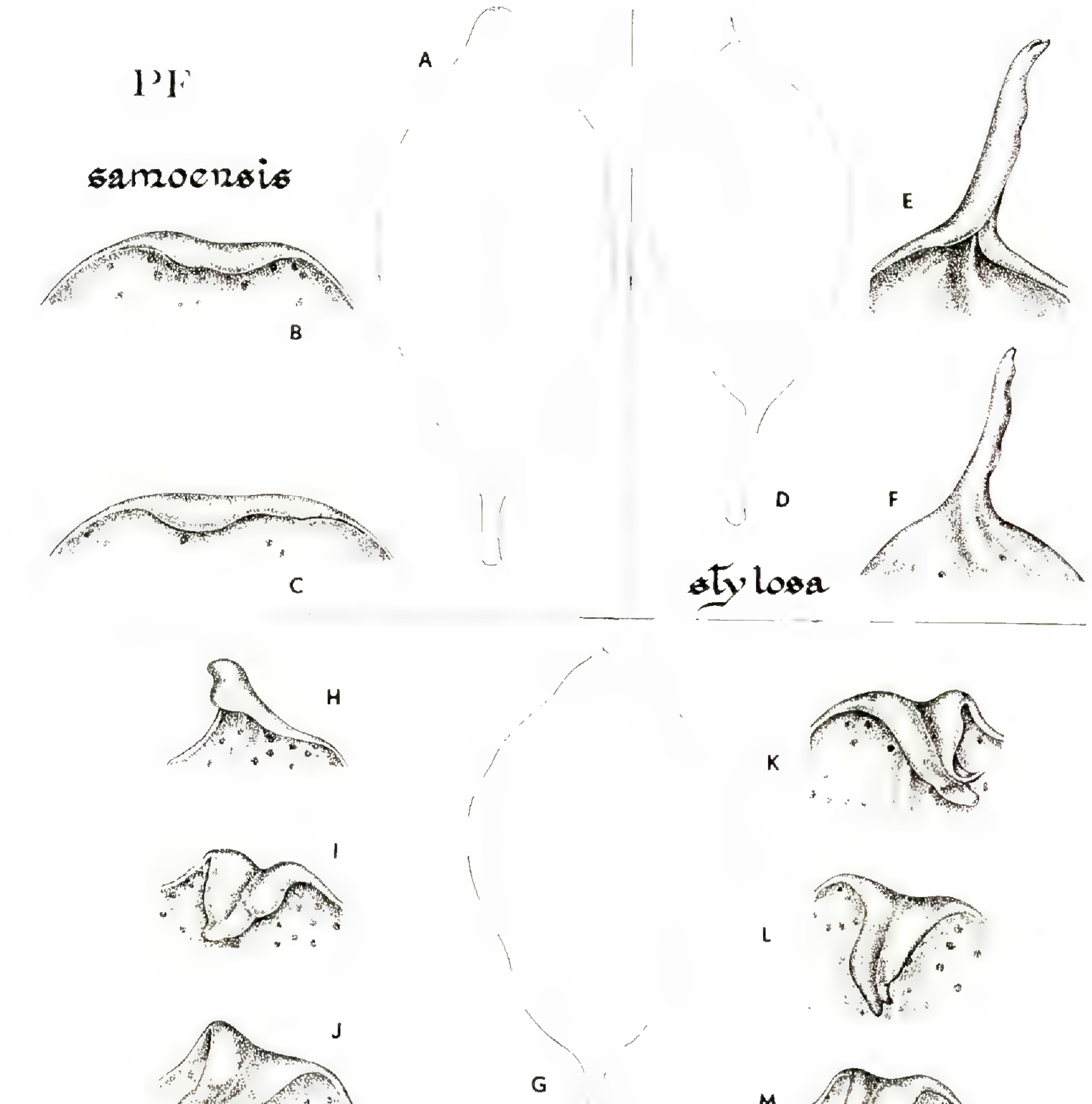
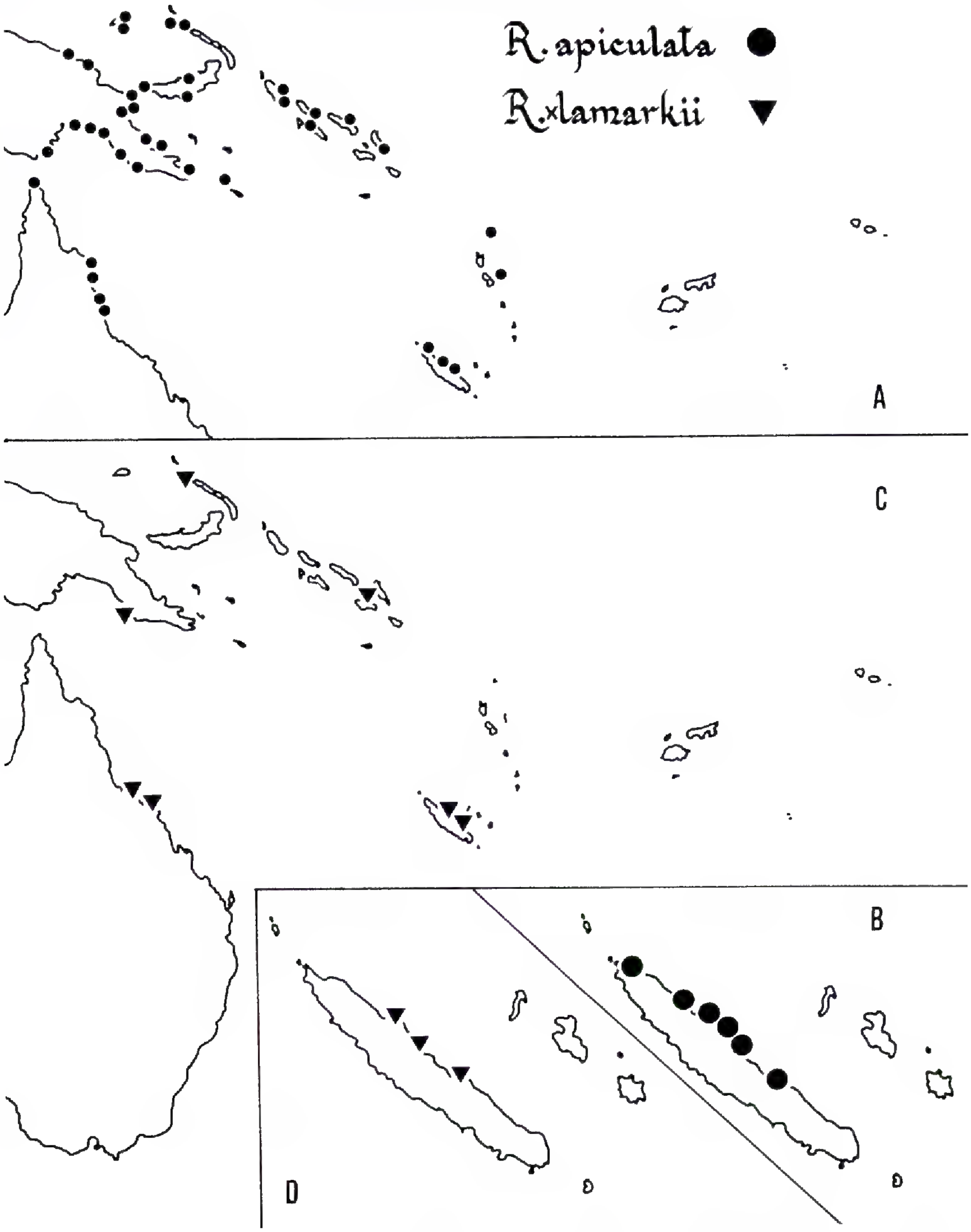
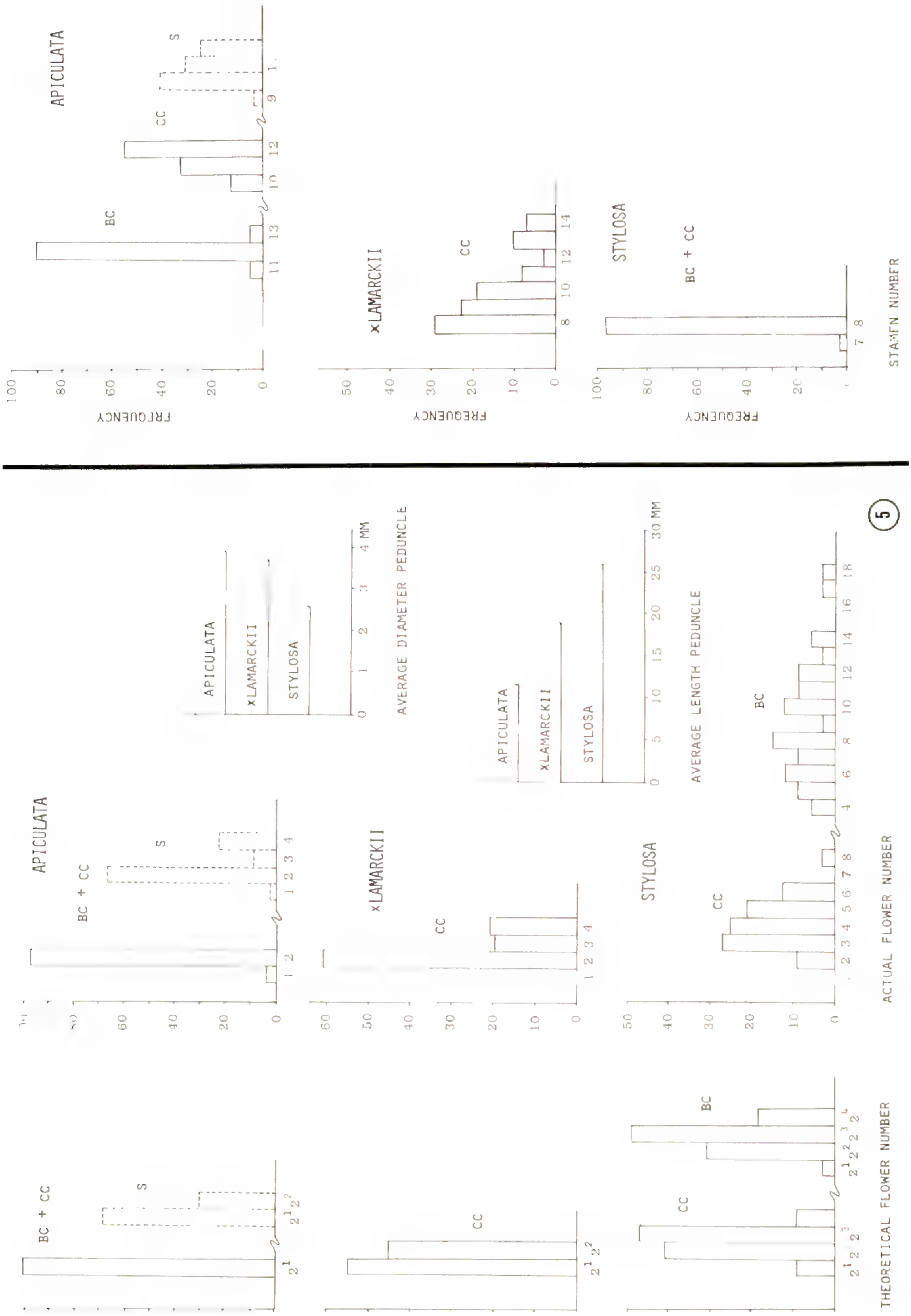


FIGURE 4. Leaf morphology of two **Rhizophora** species and their putative hybrid. A–C, *R. samoensis*: A, leaf outline, × ⅓; B, C, details of leaf with blunt recurved apex, × 5. D–F, *R. stylosa*: D, leaf outline, × ⅓; E, F, details of leaf apex with pronounced erect and persistent mucro, × 5. G–M, *R.* × *selala*: G, leaf outline, × ⅓; H–M, examples of variation in leaf apex (but always with a persistent but recurved mucro, i.e., intermediate between B, C, and E, F), × 5.



MAP 3. Distribution of **Rhizophora** in Australasia (continued), based on herbarium specimens seen by the author and field observations. A, B, *R. apiculata*: A, generalized distribution, not extending further west than New Caledonia and the New Hebrides; B, details for New Caledonia to show its apparent restriction to the northeast coast. C, *R.* × *lamarckii*, generalized distribution from all known localities (all except those in the Bismarck Archipelago based on field observations). D, details for New Caledonia. All known sites in proximity with sites of its putative parents, *R. stylosa* (cf. MAP 1, A–C) and *R. apiculata*.

The characters listed in the key might appear to be elusive, but in the vicinity of Poindimié, New Caledonia, where no less than three species together with two of their hybrids can be found growing within a few hundred meters of each other, there is no problem in naming any indi-



FIGURES 5, 6. 5, quantitative variation in certain features of inflorescence morphology in populations of some species of **Rhizophora.** Measurements are averages for about 50 samples. *R. apiculata* (above); *R.* × *lamarckii* (center); *R. stylosa* (below). Parameters represented are theoretical flower number (left), and actual flower number (center). On the right the lines compare average di-

vidual once the appropriate diagnostic features have been recognized. This demonstrates that field knowledge is essential for identifying *Rhizophora* taxa. The presence or absence of a persistent mucro will allow preliminary segregation of species. *Rhizophora apiculata* can be recognized at a distance by its larger dark green leaves, an identification confirmed at close quarters by the paired flowers borne below the leafy crown and protected by thick corky bracteoles. *Rhizophora* × *lamarckii* has leaves almost equally large, but lighter green. It never has seedlings, and its flowers are borne within the leafy crown in 4's on a rather lax inflorescence. Any remaining trees with mucronate leaf blades are *Rhizophora stylosa*; this has medium-sized flowers that are white in bud, and a lax inflorescence usually with several branch orders and more than four flowers. Although *Rhizophora mucronata* has been recorded for New Caledonia (Guillaumin, 1948) neither field nor herbarium study has revealed its presence. It would be recognizable by its sessile stigma.

The two species without a persistent mucro are much more alike, but can be distinguished by the form of the leaf apex, together with the color and shape of the flower bud, and the bracteole structure. *Rhizophora* × *selala*, in general, has longer inflorescences with more numerous flowers than *R. samoensis*.

QUANTITATIVE VARIATION

Since *Rhizophora* species are not easily distinguishable, methods were sought to quantify differences between them. Analysis of certain populations by simple biometric methods shows that although variation is large, consistent average differences do exist. FIGURES 5 and 6 summarize data from populations of *R. apiculata*, *R. stylosa*, and their putative hybrid, *R.* × *lamarckii*, mainly in Queensland. Parameters measured were:

(1) "Theoretical flower number," which is the number of nodes in the dichotomously branched inflorescence. Were every axis to terminate in a flower, this would indicate the maximum possible flower number.
(2) "Actual flower number," which is often less than the theoretical number because of abortion of certain inflorescence axes.
(3) "Stamen number," including larger aborted stamens which are quite numerous in *R.* × *lamarckii*.
(4) Average length and diameter (at half length) of the peduncle.

In these histograms the data for the Queensland *Rhizophora stylosa* ameter and length of the peduncle for the three species. Populations measured: Missionary Bay, Hinchinbrook Island, in two localities (Bowen Creek (BC) and Coral Creek (CC)) which are either combined or represented separately. For *R. apiculata* one population at Singaua, near Lae, Papua New Guinea (S, dotted outline) shown for comparative purposes. 6, quantitative variation in stamen number (including larger aborted stamens). Data from same populations as sampled in FIGURE 5.

include two sets from two different but nearby populations (CC and BC), the latter a more vigorous group of trees.

To show differences between more distant populations, the data for *Rhizophora apiculata* include measurements for a population in New Guinea characterized by quite frequent twice-branched (and therefore 3- or 4-flowered) inflorescences and flowers often with less than 12 stamens. It is not known if these differences are genetic. The general result of these histograms is to show that *R.* × *lamarckii* is intermediate between its putative parents in certain measurable characters (cf. Tomlinson & Womersley, 1976).

An attempt to produce similar histograms for *R.* × *selala* was abandoned because the differences between this species and its putative parents were smaller, and insufficient samples were measured. Precise analysis of larger populations would undoubtedly lead to quantifiable expression of differences on a statistical basis, but this morphometric approach is likely to be superseded if other diagnostically useful characters (e.g., chemical) are recognized.

CONCLUSIONS

In summary, it appears that *Rhizophora mucronata* has a restricted distribution in the western Pacific, since it is not yet known to range further east than the New Hebrides, but precise assessment of the limits of its eastward range depends on future collecting. *Rhizophora stylosa*, on the other hand, ranges as far east as Samoa, although it is not known from tropical South America. *Rhizophora apiculata* does not seem to occur further east than New Caledonia, where it is restricted to the eastern coast. *Rhizophora* × *lamarckii* clearly has a wider range in the western Pacific than hitherto appreciated, and it always occurs with its putative parents, *R. apiculata* and *R. stylosa*. *Rhizophora samoensis* extends as far as New Caledonia, and the result of this overlap between "Indo-Malayan" and "Atlantic" forms appears to be crossing with *R. stylosa* and the production of the sterile hybrid, *R.* × *selala*, in both Fiji, from where it was first reported, and (as shown here) New Caledonia.

These observations are but simple preliminaries to the larger questions about reproductive isolation between *Rhizophora* species, the breakdown of usual sterility barriers, and the apparent persistence of F_1 populations without backcrossing. Evidently more precise knowledge of the breeding mechanism of *Rhizophora* is needed. This should allow hypotheses about the origin and dispersal of *Rhizophora* in evolutionary time to be put on a less speculative basis.

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THE POTAMOGETONACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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POTAMOGETONACEAE Dumortier, Anal. Fam. 59, 61. 1829, "Potamogetoneae," nom. cons.

(PONDWEED FAMILY)

Glabrous, herbaceous, perennial or rarely annual plants of fresh or brackish waters growing entirely submersed or with both submersed and floating leaves and/or emergent inflorescences. Stems slender, branched or unbranched, often dimorphic, the lower stems rhizomatous and root-bearing, the upper erect and foliaceous, the tips often modified into turions (winter buds). Leaves alternate or subopposite, 2-ranked, entire or toothed, sessile or petiolate, stipulate, 1 to many nerved, the stipules forming a tubular sheath around the stem, free from or adnate to the base of the blade, the nerves parallel, connected by perpendicular cross-veins; submersed leaves thin, linear to orbicular; floating leaves often leathery, lanceolate, elliptic, or ovate. Inflorescence an axillary or terminal spike or panicle of spikes of perfect flowers. Perianth absent or of 4 separate, rounded, short-clawed, greenish or brownish segments in one series. Stamens 2 or 4, the anthers 1- or 2-locular, linear, dehiscing vertically, the filaments adnate to the perianth claw or absent. Gynoecium of 2–16 distinct unilocular carpels, each with a single parietal campylotropous to orthotropous, bitegmic, crassinucellar ovule. Fruit drupaceous, with a membranaceous exocarp, fleshy mesocarp, and stony endocarp. Seed solitary, basal cell of the proembryo not dividing but becoming much enlarged, the embryo straight or coiled, with a strongly developed hypocotyl; endosperm helobial in development, absent in mature seed. (Including Ruppiaceae Hutchinson, Fam. Fl. Pl. 2: 48. 1934, nom. cons. Excluding Zannichelliaceae Dumortier, 1829; Zosteraceae Dumortier, 1829, nomina conservanda.) TYPE GENUS: *Potamogeton* L.

[1] Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum of Harvard University made possible through the support of the National Science Foundation. This treatment, the eighty-fourth in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296–346. 1958). The area covered includes North Carolina, South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to plants of this area, with supplementary information in brackets. References that I have not seen are marked by an asterisk.

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The illustration of *Ruppia* was drawn by the late Dorothy H. Marsh under Dr. Wood's direction largely from material collected by Dr. R. B. Channell in Harrison County, Mississippi; that of *Potamogeton* was drawn by Karen S. Velmure under my direction from material that I collected in Alabama.

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A family of nearly cosmopolitan distribution with three genera and about 110 species. Two genera, *Potamogeton* and *Ruppia*, occur in the southeastern United States. *Groenlandia* J. Gay (*G. densa* (L.) Fourr., *Potamogeton densa* L.) is native to western Europe, North Africa, and southwestern Asia. Members of the Potamogetonaceae have been placed in the Najadaceae by Eyles & Robertson, Fassett, and Gleason (in Gleason & Cronquist) and have been combined with members of Zannichelliaceae and Zosteraceae by den Hartog, Fernald, and N. Taylor to comprise a taxon that has been called respectively Potamogetonaceae, Zosteraceae, and Zannichelliaceae. The Potamogetonaceae, as here interpreted, are separated from the Zannichelliaceae and Zosteraceae by their perfect flowers, lack of a spathelike bract, and, in some species, the presence of turions. Thorne's order Zosterales includes Aponogetonaceae, Juncaginaceae, Potamogetonaceae (including *Ruppia*), Posidoniaceae, Zannichelliaceae, and Zosteraceae.

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KEY TO THE GENERA OF POTAMOGETONACEAE IN THE SOUTHEASTERN UNITED STATES

Stamens four; perianth present; stipule free from leaf blade or, if adnate, with the tip free; fruits sessile or very short stalked (see FIGURE 1). . . . . 1. *Potamogeton.*

Stamens two; perianth absent; stipule adnate to leaf blade for entire length (without free tip); fruits long stalked (see FIGURE 2). . . . 2. *Ruppia.*

1. **Potamogeton** Linnaeus, Sp. Pl. 1: 126. 1753; Gen. Pl. ed. 5. 61. 1754.

Annual or perennial, glabrous, herbaceous plants growing submersed in fresh (rarely brackish) waters, propagated by seeds, turions, or rhizomes. Stems varying in length with water depth, branched or unbranched, terete or compressed, rooting at lower nodes, the nodes occasionally with

oil glands. Leaves submersed or both submersed and floating, alternate to subopposite; submersed leaves pellucid, sessile or petiolate, linear to orbicular, subulate to obtuse at apex, acute to perfoliate at base, the margins entire or serrate, rarely crimped, the veins 1–35; floating leaves coriaceous, mostly petiolate [rarely subsessile], elliptic to ovate, acute to obtuse at apex, cuneate to rounded or cordate at base, the margins entire, the veins 1–51; stipules tubular, sheathing the stem and young inflorescences, connate or convolute, either free or adnate to the base of the submersed leaves, free from base of floating leaves. Turions (winter buds) present or absent, with extremely shortened internodes, divided into inner and outer leaves; the inner few to numerous, rolled into a fusiform structure or unmodified [shortened and oriented at 90° angles with respect to outer leaves]; the outer 1–5 per side, mostly similar to vegetative leaves [corrugated near base]. Inflorescence axillary or terminal, a capitate or cylindrical spike or panicle of spikes with 1–20 whorls of flowers, compact or moniliform, with 2–4 flowers in each whorl, submersed or held above surface of water. Perianth of 4, free, rounded, short-clawed segments. Androecium of 4 stamens, the filaments adnate to the perianth claw, the anthers 2-locular, extrorse, the tapetum amoeboid, the pollen spherical to fusiform, sculptured, 3-celled. Gynoecium of 4 carpels, the ovule orthotropous or campylotropous, the micropyle formed by the inner integument. Fruit dorsally rounded or keeled, beaked. Embryo coiled 1 or more times. Chromosome base number 13 or 14 (Stern). TYPE SPECIES: *P. natans* L.; see N. Taylor, N. Am. Fl. 17: 14. 1909. (Name from Greek, *potamos*, river, and *geiton*, neighbor.) — PONDWEED.

A genus of perhaps 100 species, in two subgenera, POTAMOGETON and COLEOGETON, both almost cosmopolitan in distribution, and both divided into two sections; represented in the United States by 31 species, some widely distributed, 15 occurring in our area.

Subgenus POTAMOGETON (peduncle mostly rigid and rarely with an endodermis, stigmatic papillae small, pollination mostly by wind), sect. ADNATI Hagström (stipules adnate for one-half their length to the leaf bases, inflorescence a panicle of spikes), apparently is represented in our area by a single collection of *P. Robbinsii* Oakes, $2n = 52$, from the Mobile delta in southwestern Alabama. Although this species occurred in northwestern Georgia at the height of the most recent glaciation (ca. 20,000 years B.P.) (see Watts), its present range is far to the north (from New Brunswick, south only to Delaware, and west to Washington and Oregon). Whether or not a mistake in labeling is involved in the Alabama record is uncertain. *Potamogeton Robbinsii* is easily recognized by its auriculate leaf bases and its inflorescence, a panicle of spikes. Section AXILLARES Hagström (stipules free or adnate for less than half their length, inflorescence a simple spike) consists of about 85 species, mostly of the Eastern Hemisphere. Thirteen species occur in our area: *P. crispus* L. (introduced), *P. amplifolius* Tuckerman, *P. pulcher* Tuckerman, *P. nodosus* Poiret (*P. americanus* Cham. & Schlecht., *P. lonchites* Tuckerman, *P. fluitans* sensu

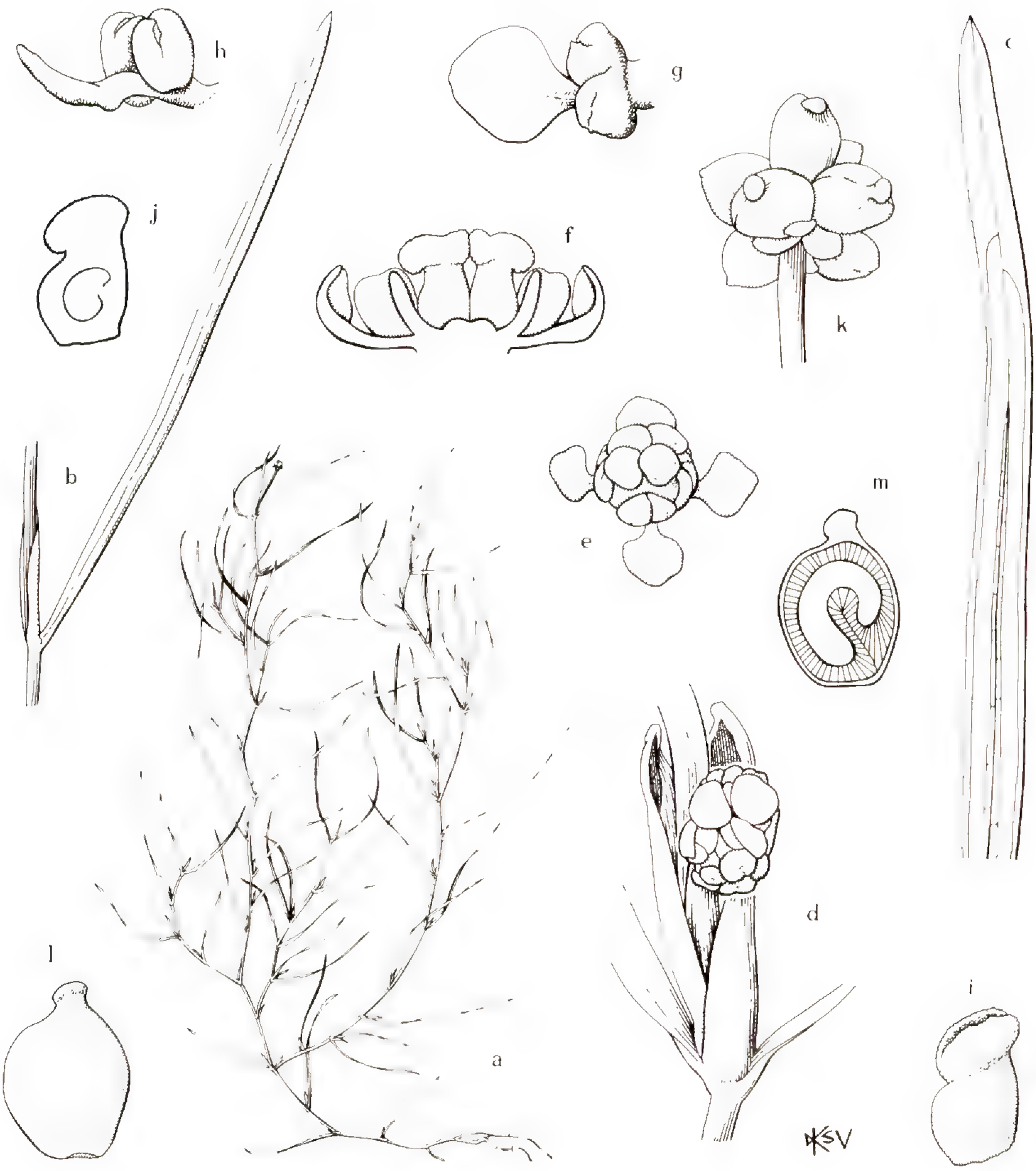

FIGURE 1. **Potamogeton** section **Axillares.** a–m, *P. pusillus* (*P. Berchtoldii*). a, habit of plant, × ½; b, leaf with stipule, × 5; c, detail of leaf blade to show venation, × 12; d, young inflorescence with two flowers, tepals unshaded, × 10; e, flower, seen obliquely from above, four tepals, three stamens, and four carpels visible, × 10; f, flower in vertical section to show relationship of stamens to tepals (two stamens cut in half) and two of four carpels, × 20; g, tepal with stamen, from above, × 20; h, same, from the side, × 20; i, carpel, side view, at anthesis, × 20; j, carpel in vertical section (diagrammatic) to show single parietal campylotropous ovule, × 20; k, infructescence, × 6; l, single drupe, side view, × 10; m, same, in vertical section, endocarp hatched, embryo unshaded, × 10.

Small), *P. natans* L., *P. illinoensis* Morong (*P. angustifolius* and *P. lucens* sensu American authors), *P. perfoliatus* L., *P. diversifolius* Raf. (*P. capillaceus* Poiret), *P. epihydrus* Raf. (*P. Claytonii* Tuckerman, *P. Nuttallii* Cham. & Schlecht., *P. cayugensis* (Wieg.) Hagström), *P. tennesseensis*

Fern., *P. confervoides* Reichenb. (*P. Tuckermanii* Robbins), *P. foliosus* Raf. (*P. Curtissii* Morong, *P. niagarensis* Tuckerman, *P. pauciflorus* Pursh), and *P. pusillus* L. (*P. Berchtoldii* Fieber, *P. panormitanus* Biv., *P. lacunatus* Hagström). The exact nature of *P. floridanus* Small, based on two collections made by A. H. Curtiss in 1886 (NY) is uncertain (cf. Ogden, 1943, p. 192).

Subgenus COLEOGETON (Reichenb.) Raunk. (peduncles mostly flexible and with an evident endodermis, stigmatic papillae large, pollination mostly by water), section CONVOLUTI Hagstr. (sclerenchyma abundantly developed, stipule sheaths convolute) is represented in the southeastern United States by *Potamogeton pectinatus* L. (*P. columbianus* Suksdorf, *P. interruptus* Kit.), $2n = 78$, which occurs almost throughout the United States. It can be distinguished from other pondweeds by its stipules adnate nine-tenths of their length to the leaf blade and by its fruits with an evident beak. Section CONNATI Hagstr. (sclerenchyma poorly developed, stipule sheaths connate) is widespread in the northern United States and Canada but is not represented in our area.

The characters important in determining the various taxa of *Potamogeton* are found in the fruiting spikes, fruits, leaves, and turions. Among the most distinctive features of the fruits are the size and shape (whether widest at, above, or below the middle), the absence or presence and shape of keels on the dorsal surface, and the degree of coiling of the embryo. Important characters of the fruiting spike include its position (terminal or axillary), its shape (globose, cylindrical, or moniliform), the number of fruits per spike, and the anatomy of the peduncle. Distinctive features of the leaves include the presence or absence of floating leaves, the degree of adnation of the stipule with the blade of submersed leaves, the number of major veins, and the presence or absence of lacunae bordering the midrib of submersed leaves. Evident characteristics of the turions, if present, include the shape of the inner as compared with the outer leaves, and the time of year the turions germinate. Although several vegetative characteristics can be used for identifying the taxa of *Potamogeton*, characters of the fruits and peduncles are the most important ones, and care should be taken to collect only specimens with at least partially mature fruit.

The anatomy of *Potamogeton* has been studied by Ogden (see family references) and Singh (1964). According to Ogden, the stele is composed of fibrovascular bundles, mechanical tissue, and parenchyma cells. The arrangement of the bundles varies with the species. Four patterns can be recognized: 1) proto-type — bundles free, each with one patch of phloem, four median bundles, and a few smaller bundles along the sides; 2) trio-type — three of the median bundles fused to form a single xylem canal, with one patch of phloem on the outer face of the xylem canals and one or two on the inner face; 3) oblong-type — one or two median bundles lacking phloem on each side and with the stele oblong or elliptical in cross section; 4) one-bundled type — only a single bundle, this with four patches of phloem which often are not evident. The stem usually has an endodermis in which the cells are either O-cells having the wall of uniform

thickness, or U-cells in which the walls are thickened on the inner and lateral faces but thin on the outer face. The cortex, which is highly lacunate, may be without vascular bundles or fibers, or with vascular bundles and fibers, or only with fibers at some junctures of the chains of cells separating lacunae. According to Singh, cells of both the upper and lower epidermis have slightly thickened outer tangential walls. On floating leaves the upper epidermis has stomata and a distinct cuticle; submersed leaves lack stomata.

The flowering structures of *Potamogeton* have been interpreted variously. Miki, Uhl, and Eames have considered each perianth segment to be a sepaloid bract subtending and adnate to the corresponding stamen and have therefore regarded the flower as an inflorescence of four staminate flowers, each with a single stamen and its adnate bract, and four apetalous carpellate flowers, each of a single carpel with one ovule. In this interpretation, the spike represents a reduced compound inflorescence. Singh (1965), on the basis of the vascular anatomy and floral morphology of seven species of *Potamogeton*, chose to consider the flower a normal one with four perianth segments, but Sattler (1965) considered it impossible to classify the structure as either a true flower or an inflorescence, because it displayed characters of both. Sattler questioned the classical use of flower and inflorescence as two separate categories and emphasized the need for more developmental work in the Helobiales (Alismatidae). For the sake of convenience, Singh's concept is followed in this treatment.

Controversy has also existed as to the real nature of the perianth-like structures that are adnate to the stamens. Irmisch (1851), Ascherson (1889), Rendle (1930), and Markgraf (1936) considered the segments to be stamen connectives (outgrowths of the stamens), but both Sattler (1965) and Singh (1965) reached a different conclusion. Sattler, for example, demonstrated that in *Potamogeton Richardsonii* these structures are initiated on the floral apex before the stamens and thus cannot be outgrowths of them. He instead considered them to be perianth segments. After inception of the stamen primordia, growth occurs between the perianth primordium and that of the stamen, thereby uniting the base of the developing stamen and perianth segment.

Taxonomic difficulties in the genus are due in part to vegetative plasticity and to hybridization within the genus. Hunt (1962) and Haynes (1974) have reported that certain populations of narrow-leaved pondweeds show seasonal dimorphism. Other dimorphisms occur when populations occupy habitats different from the normal. Fernald separated *Potamogeton foliosus* into two varieties based on size, but Haynes (1974) suggests that these are only different growth forms, plants in flowing waters usually being much larger than those growing in standing waters. In addition, many floating-leaved species produce terrestrial forms that remain after the lake, pond, or pool in which they were growing dries. Reznicek & Bobbette indicate that the terrestrial forms of the *P. diversifolius* alliance are often nearly impossible to identify.

Taxonomic problems within the genus are compounded by numerous

populations of hybrids intermediate between their two putative parental species. These hybrids, although usually sterile, often form extensive populations by vegetative reproduction from rhizomes or turions. Hagström, Ogden (1943), Haynes & Williams, and Hellquist (pers. comm.) have reported probable hybrid populations.

The reproductive biology of the genus is largely unstudied. Most species are considered to be wind pollinated, but Thieret (pers. comm.) has noted that dragon flies have been observed to land on *Potamogeton nodosus* spikes. Although after the insects were collected, Thieret and his students observed pondweed pollen on them, there is no evidence that the insects actually accomplished pollen transfer to another inflorescence. It is not known whether some or all species are self compatible, but some that are considered to be wind pollinated have produced fruit during seasons in which the inflorescence never reached the surface of the water (Voss, 1972). Some appear to flower regularly under water and are presumably water pollinated.

According to Sculthorpe, certain species of *Potamogeton* reproduce by rhizome fragments, tubers, or turions. In some, the stem apex is modified by shortening of the internodes into turions that break off and eventually grow to produce new members of the clone. Turions can result in a phenomenal increase in the population, as shown by Yeo, who planted one turion of *Potamogeton crispus* on 1 April 1963 and found at the end of the growing season that 23,250 turions had been produced! In other species vegetative propagation is by fragmentation of the rhizome or by fragmentation of tubers from the rhizome.

All species reproduce to a certain extent by seeds. Muenscher (1936) demonstrated that the germination rate of *Potamogeton* seeds is greatly reduced by drying. Many species, according to Muenscher, require near-freezing temperatures for a period of one to three months. However, as shown by Sullivan for many of the broad-leaved species, the fruits can be induced to germinate without a previous cold treatment if the exocarp and mesocarp are split. The fruits of many pondweeds are among the most common foods of waterfowl (Martin & Uhler), which often digest only the exocarp and mesocarp, the endocarp with the intact seed being passed from the digestive system. Lohammar has shown that a high percentage of germination may follow.

The genus is economically important as a source of food for wildlife. For waterfowl Martin (1951) and Martin & Uhler rank it first in importance in the United States and Canada, and Gaevskaya lists 124 species of animals that have been known to feed on the genus. In addition, populations of *Potamogeton* have often been abundant enough in the southeastern United States to be regarded as weeds warranting the use of various methods of control.

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2. Ruppia Linnaeus, Sp. Pl. 1: 127. 1753; Gen. Pl. ed. 5. 61. 1754.

Glabrous, herbaceous, annual or perennial plants growing submersed in brackish or saline waters. Stems slender, terete, branched or unbranched, rooting at the lower nodes. Leaves all submersed, alternate to subopposite, sessile, divided into blade and stipular sheath; blade linear or setaceous, 1-nerved, the margins entire below, minutely serrulate above, the apex acute to truncate; stipular sheath formed by adnation of stipule to blade for entire length of stipule. Turions absent [present with one internode, the leaves undifferentiated]. Inflorescence a 2-[1- to few-]flowered

capitate spike, at first enclosed by sheathing leaf bases; peduncle elongating at anthesis, elevating the inflorescence to or near the water's surface, often becoming spirally twisted in fruit, then pulling the developing fruit below the surface. Perianth absent. Androecium of 2 sessile anthers, the two 1-loculate halves separated by a broad connective, the dehiscence extrorse, the tapetum amoeboid, the pollen elongate, 4 times as long as broad, arcuate, swollen at the ends and at the center on the convex side, 3-celled, the exine reticulate, exceedingly thin, discontinuous at the swellings, the intine rather thick, further thickened in the swollen regions. Gynoecium of 4 or 5 [2–16] distinct, stipitate [sessile] carpels, the gynophore (stipe, podogyne) elongating after anthesis, the placentation parietal, the ovule campylotropous, the micropyle formed by both integuments. Fruit asymmetrical, dorsally rounded [or with a prominent transversely ridged crest], beaked [or beak absent], long stipitate [or sessile], the exocarp and mesocarp often decaying leaving the operculate endocarp intact. Embryo straight. TYPE SPECIES: *R. maritima* L. (Name dedicated to Heinrich Bernhard Ruppius, 1689–1719, a German botanist.) — DITCH-GRASS.

An almost cosmopolitan genus of perhaps 10 species, represented in the United States by *Ruppia maritima* L., widgeon-grass, $2n = 20$, which occurs along the coast from Maine to Texas, then sporadically inland to Michigan, California, and Washington.

The characters important in determining the various taxa of *Ruppia* are based on the fruits (whether strongly asymmetrical or only slightly so); the carpels (4, 5, or 8–16); the gynophore (slender, stout, or absent); the shape of the leaf apex (acute, obtuse, or retuse); the cross sectional structure of the leaf (shape of the lacunae and number of cells separating the lacunae from the epidermis); and the presence or absence of turions.

The genus is poorly understood both taxonomically and ecologically, and a thorough revision utilizing data from ecology, chemistry, and cytology, as well as morphology, is needed. (See Reese.)

According to Ogden (see family references), the anatomy of the stem and peduncle is very similar to that of the narrow-leaved species of *Potamogeton*. There is a stele with a single vascular bundle, an endodermis of O-cells, and a cortex without interlacunar or subepidermal bundles. The leaf has a central vein with a lacuna on both sides running the entire length of the blade.

In their paper on the floral development of *Ruppia maritima*, Posluszny & Sattler investigated the development of "the small dorsiventral outgrowth on its stamen connective." (See FIGURE 2, e, h, i.) Contrary to previous conclusions that these outgrowths are homologous with the sterile appendages (tepals) of the *Potamogeton* flower, they found that ". . . developmental studies reveal a most remarkable difference between *Potamogeton* and *Ruppia*. In *Potamogeton* the appendages are initiated acropetally on the floral apex and develop like typical phyllomes (Posluszny and Sattler, 1973, 1974). In contrast . . . in *Ruppia maritima* the

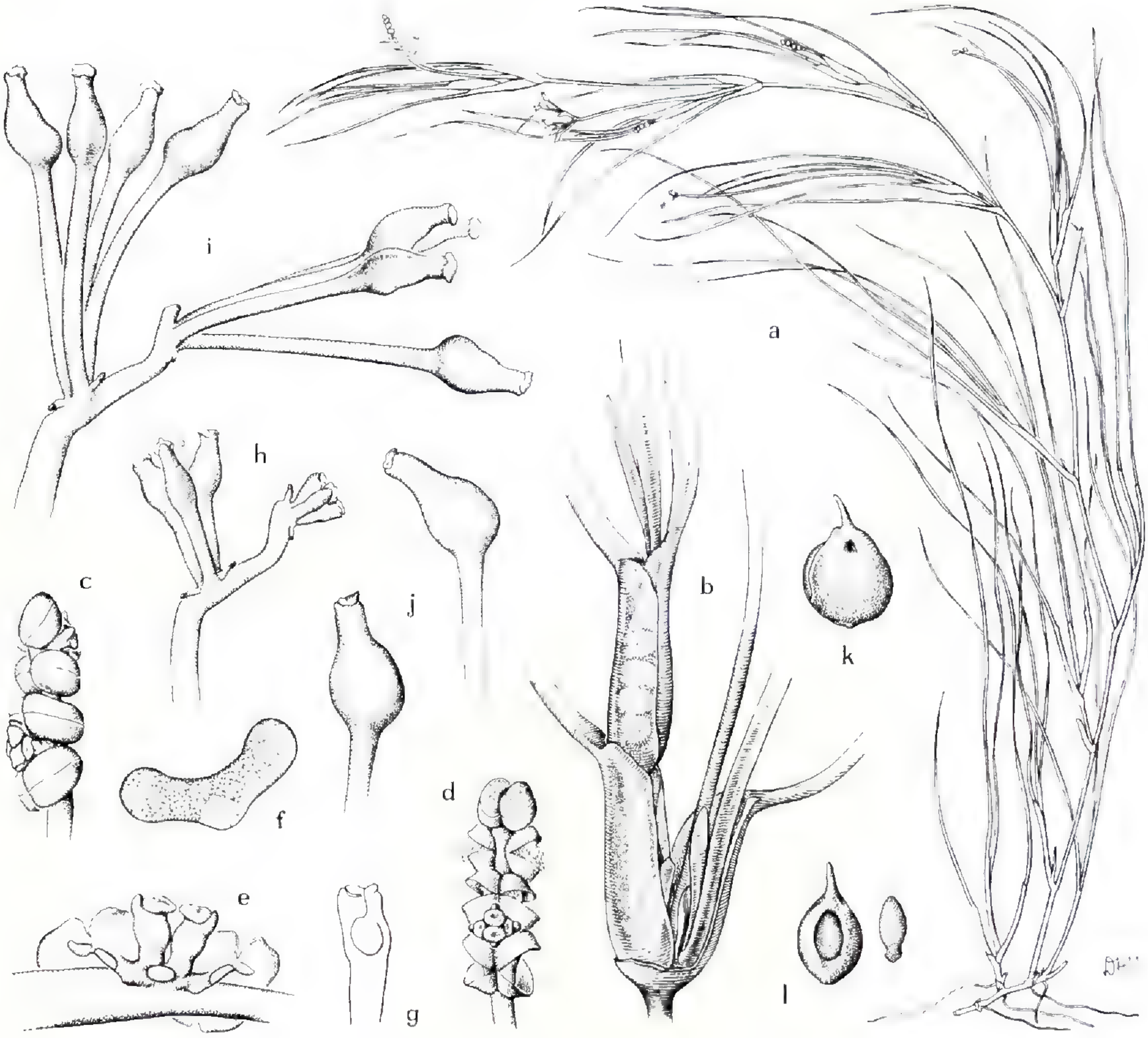

FIGURE 2. **Ruppia.** a–l, *R. maritima.* a, portion of plant with flowers and young fruit, × ½; b, tip of shoot to show sheathing leaves (stipules completely adnate) inclosing inflorescence, above, and stipular sheath (sheath at right partially cut away), two young leaves, and peduncle of inflorescence, below, × 3; c, inflorescence, side view, showing two flowers facing in opposite directions, each flower with four carpels and two stamens, × 5; d, inflorescence, from above, at anthesis, pollen already shed from stamens of lower flower, × 5; e, lower flower, side view, with two carpels and two half-anthers removed, × 10; f, pollen grain, side view, × 330; g, carpel shortly after anthesis, in vertical section (diagrammatic) to show ovule, carpel oriented as left carpel in "e," × 10; h, inflorescence with developing carpels (flower to left), the gynophores elongating, and unfertilized carpels (flower to right), × 5; i, partially mature fruits of two flowers, × 5; j, two mature drupes, × 5; k, endocarp, side view, lid to left, × 5; l, endocarp, adaxial side, with lid removed, lid to right, × 5.

connective outgrowth develops, unlike either a tepal or a bract, after stamen inception, in fact after the beginning of theca differentiation. It results from growth very slightly abaxial to the tip of the stamen connective. Although it becomes dorsiventral, it . . . lacks any vascularization at maturity. In general, it is similar to a vertical extension of the stamen connective in *Potamogeton* [*Groenlandia*] *densus* (Posluszny and Sattler, 1973), and may be considered homologous with the latter. . . . Carpel development is similar in *Ruppia* and *Potamogeton*. . . . Many who have made comparisons of vegetative appendages, mature flowers, and seeds

(Markgraf 1936; Uhl 1937; Singh 1965; Gamerro 1968) claim that *Ruppia* is closely related to *Potamogeton*. [Floral development] does not contradict it, but it certainly does not bring the two genera closer together. . . . The floral development of *R. maritima*, though, does fit into a trend of simplification and reduction between *Potamogeton* and *Zannichellia*, as noted by Singh (1965). According to this trend, reduction occurs in the number of appendages per flower, flowers per inflorescence, and vegetative appendages on the renewal shoots before floral induction."

The observations of Gamerro on the floral biology of *Ruppia cirrhosa* in Argentina are summarized below. Flowering begins by the opening of the leaf sheath which surrounds the developing inflorescence. This usually occurs in the afternoon and is followed by peduncle elongation, which is by cell enlargement alone, since no meristematic tissue is present. During the daylight hours of the first day, the peduncle usually elongates as much as 2 cm., and that night much greater elongation occurs (in most instances), pushing the inflorescence to the surface of the water. Usually very little emergence takes place, for the peduncle bends and lies horizontal just below the surface. In any case, there is a film of water surrounding the inflorescence. Occasionally elongation may occur on the second, instead of the first, night.

Pollen release occurs during the morning following elongation. Opening of the anther locule is indicated by the appearance of bubbles, mostly oxygen, at a line of abscission of each anther half from the connective. The bubbles continue to enlarge and become confluent until abscission is complete. At this time, the bubble, about twice the size of the anther half, carries it to the surface of the water. As the anther half contacts the atmosphere, it opens violently, spreading the pollen over the surface of the water, with clusters of grains adhering end to end, forming chains. The pollen grains are oriented with the concave cavity upward, and bubbles trapped in the cavity and reticulation of the exine keep the pollen chains afloat. Dehiscence of the anther half occurs by the curving of the walls downward and the edges inward. At the same time, the anther half remains afloat by the spreading over the surface of the water of an internal cutinized membrane.

Following pollen release, growth of the peduncle resumes, but the inflorescence, which has now been reduced to two apocarpous gynoecia, remains just below the aqueous film surrounding the pollen grains. The apex of the inflorescence curves slowly so that the carpels of the lower flower are inclined forward, the gynoecia of both flowers then being in line with the axis of the inflorescence. Gamerro could not positively determine the time at which the stigmas are receptive to pollen, but it appears that the flowers are probably protandrous. The straightening of the inflorescence is complete within 24 hours of pollen release.

Within two or three days after pollen release, spiraling of the peduncle begins from its base upward. Spiraling is accomplished by the unequal enlargement of cells, the exterior ones enlarging more than the interior. As a result of the spiraling, the carpels are pulled deeper into the water

and are oriented toward the substrate. The spiraling process, which may occur with or without pollination, is completed within three or four days. Gynophore elongation, which occurs shortly after the spiraling process is complete, takes approximately seven to eight days to complete. This elongation, unlike spiraling, is dependent on fertilization. (Cf. FIGURE 2, h.) The fruits are mature within 15 days after gynophore elongation. The entire process is complete within 30 days after the inflorescence emerges from the leaf sheath.

Ortu, studying the influence of temperature and salinity on the germination of seeds of *Ruppia maritima*, has observed that sodium chloride in concentrations of 52 grams/liter generally inhibits germination; that the dormant period decreases with increase of temperature; and that at 30° C. seeds kept in solutions of 3.5 grams/liter have a higher germination rate, whereas at 20° C. a higher germination rate is observed among those kept in solutions of 6.5, 13, and 26 grams/liter.

Economically, the genus is important only as a source of food for waterfowl and other wildlife. Gaevskaya lists 14 species that have been known to feed on *Ruppia*.

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THE NODAL ANATOMY OF MYROTHAMNUS FLABELLIFOLIUS (MYROTHAMNACEAE): ANOTHER EXAMPLE OF A "SPLIT-LATERAL" CONDITION

CHRISTIAN PUFF

IN 1970, HOWARD SUGGESTED the "split-lateral" or "common gap" condition as another type of nodal anatomy worthy of recognition. In his review he reported that members of the Asteraceae, Caprifoliaceae, Chloranthaceae, Gentianaceae, Gesneriaceae, Rhizophoraceae, Rubiaceae, and Zygophyllaceae have "split-laterals." To his list I can add the Myrothamnaceae, a monotypic family often associated with the Hamamelidales, but also considered in connection with the Magnoliales.[1]

MORPHOLOGICAL DESCRIPTION

The branches of the shrubby *Myrothamnus flabellifolius* show a clear differentiation into long and short shoots and bear decussately arranged leaves which exhibit a number of peculiarities.[1] The following characters are essential for an understanding of the vascularization pattern of the plant.

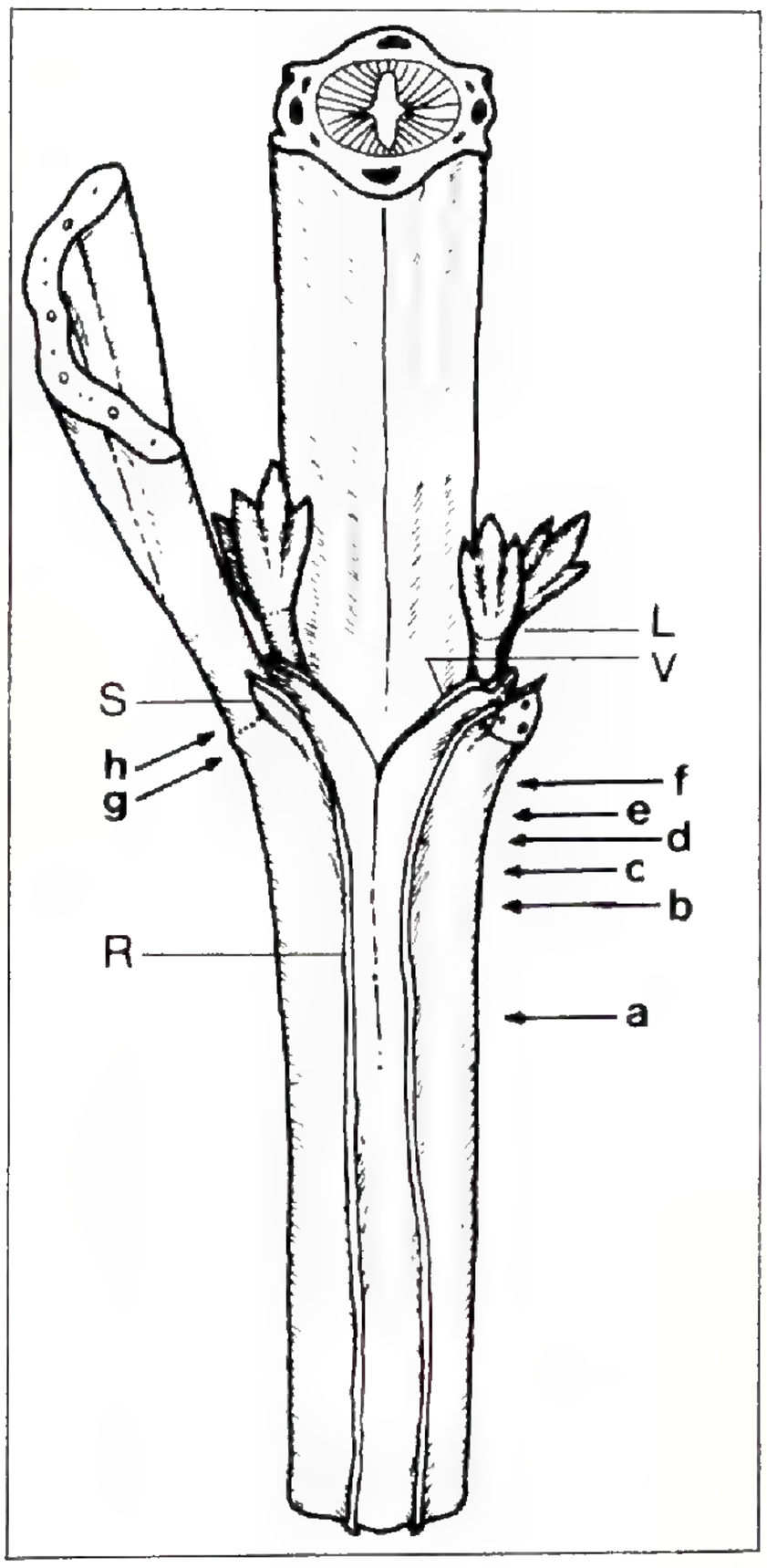
The "Unterblätter" (leaf bases) of each pair of opposite leaves are fused (gamophyllous) and form a sheath which remains on the shoot after the "Oberblatt" (leaf blade) has abscised (see FIGURE 1, insert: the dotted line between "g" and "h" marks the position of the abscission zone). In short shoots, the "Unterblätter" remain rather small (ca. 1.5 mm.), are tightly packed, and overlap considerably — a single section through a short shoot may hit as many as three pairs of leaf bases (also see Puff, 1978, *fig. 4b*). In long shoots (FIGURE 1, insert) they appear much longer; a short distance from a node downward, however, they fuse with the stem, making a distinction between leaf and stem impossible (see FIGURE 1, sections a–c). They bear two kinds of appendages: four lateral ridges (FIGURE 1, insert: R) which run down the whole length of the internode and terminate as "stipules" or stipule-like appendages (FIGURE 1, insert: S) just below the abscission zone; and adaxially, between leaf base and stem, the "vaginal" or "median" lobes (FIGURE 1, insert: V), which often envelop newly developed lateral shoots (FIGURE 1, insert: L).

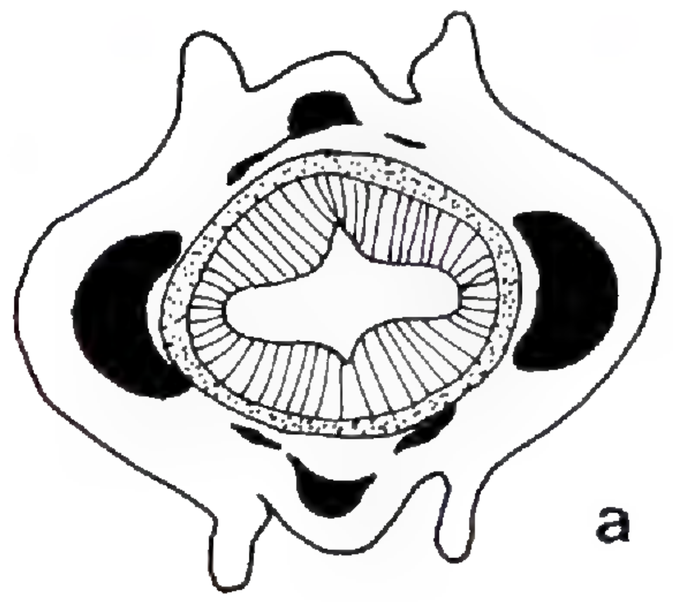
VASCULARIZATION PATTERN

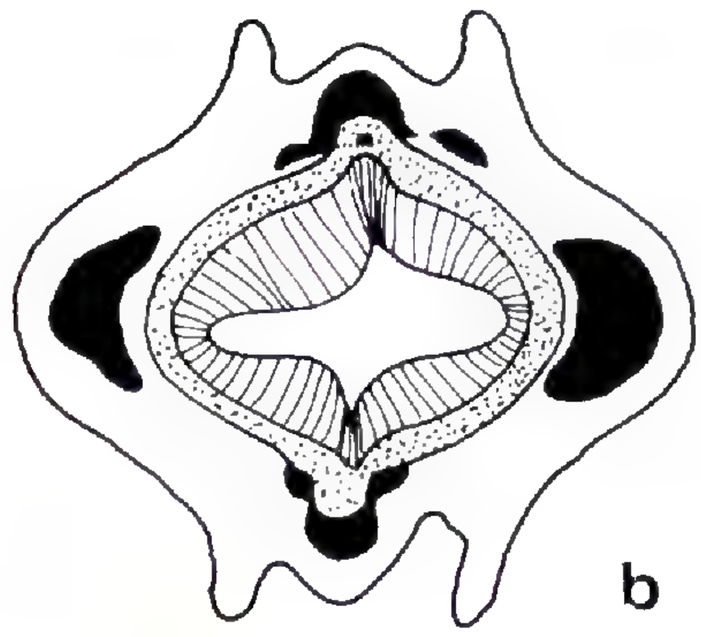
For the sake of greater clarity, consecutive sections cut through a long shoot are presented in FIGURES 1 and 2.[2]

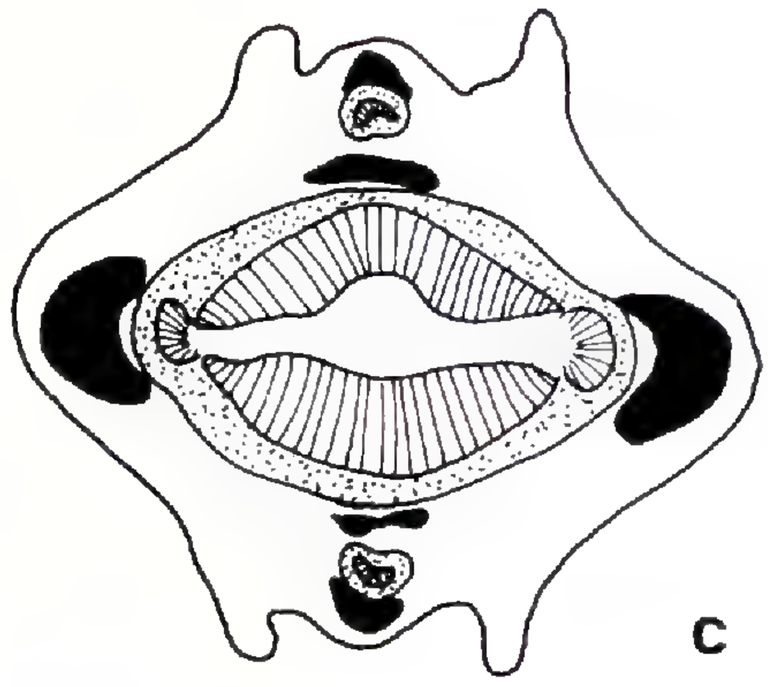
[1] For a recent compilation of our knowledge of *Myrothamnus*, see Puff (1978).

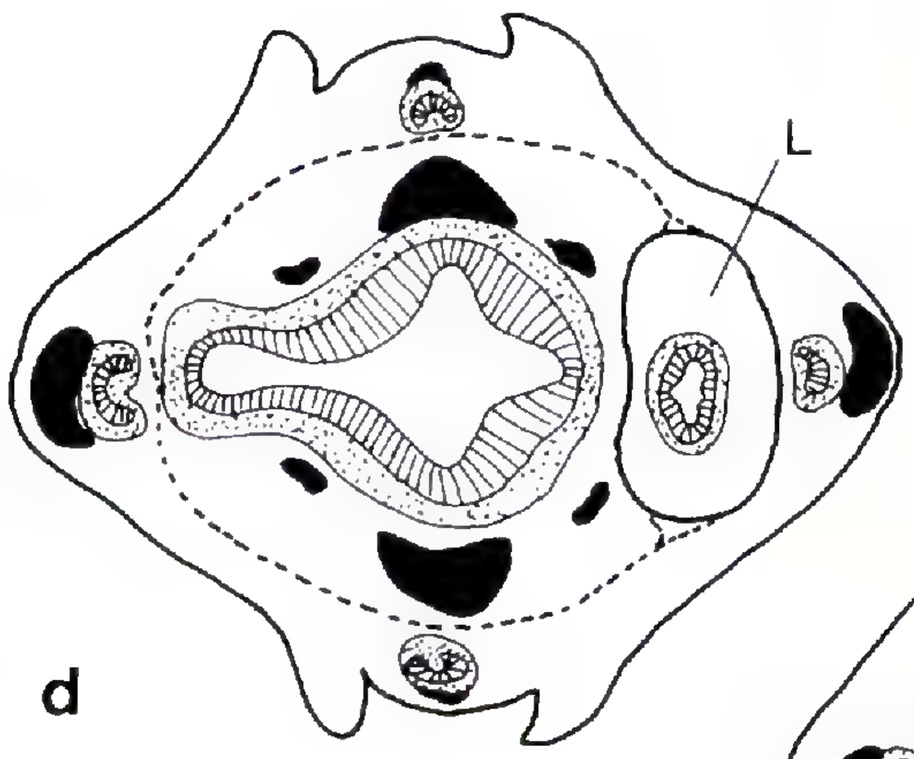
[2] The vascularization pattern of short shoots is not different, but is much more difficult to interpret because of the short internodes and the overlapping, tightly packed "Unterblätter."











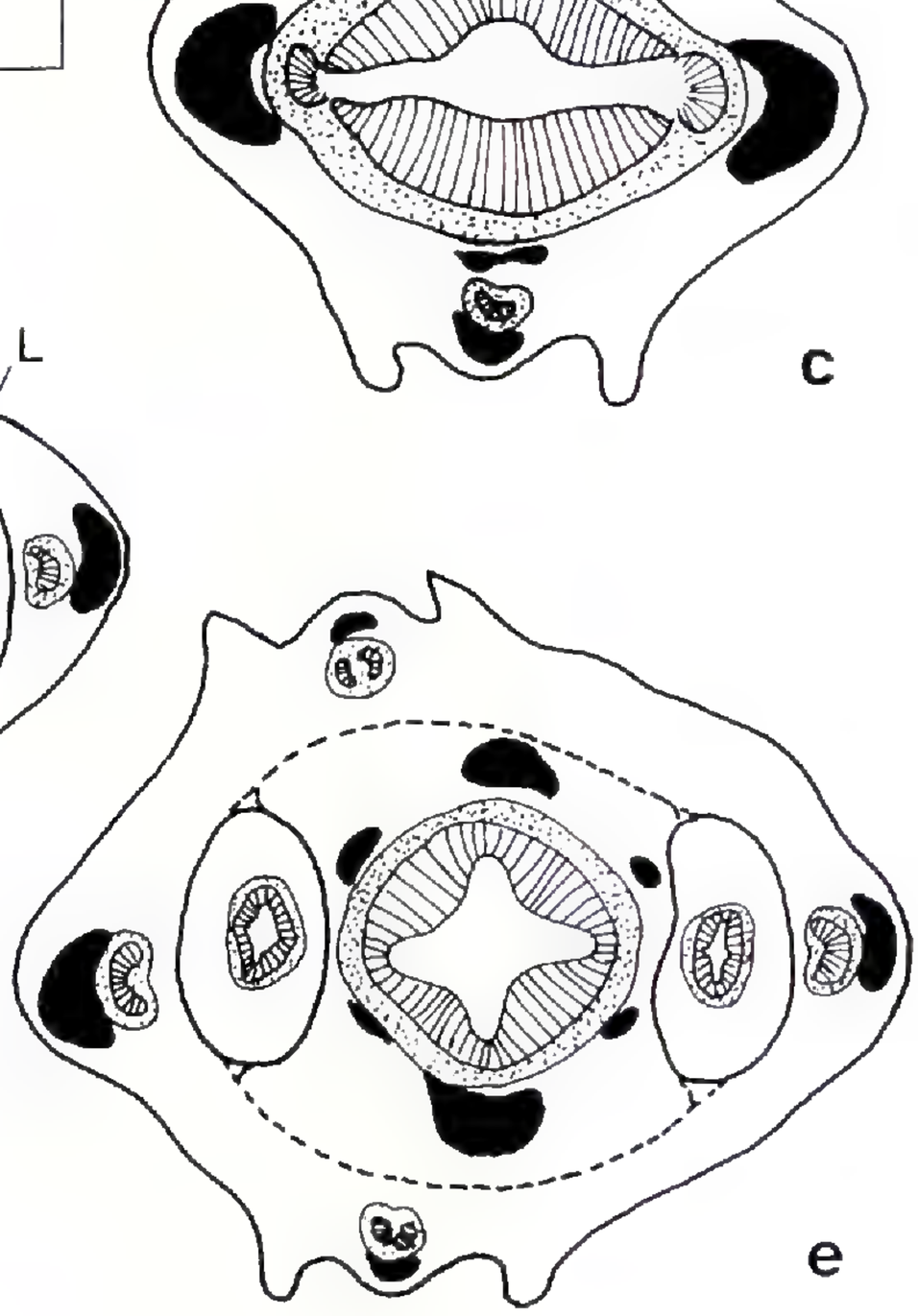


FIGURE 1. **Myrothamnus flabellifolius.** a–e: camera lucida drawings of sections through a long shoot. Insert: portion of a long shoot; arrows indicate where sections a–e and f–h (FIGURE 2) were cut. Black areas: sclerenchymatic tissue; hatched areas: xylem; dotted areas: phloem.

Sections a–c show the characteristic four ridges that, starting at the abscission zone, run down the whole length of the internode; they are not vascularized. At the level of sections a, b, and c, no differentiation can be made between "leaf" and "stem" in spite of the presence of these ridges. Massive sclerenchyma strands run through the cortex in the median; two somewhat smaller ones (each of them accompanied by a small band on either side) are in the area between two adjacent ridges (section a).

At a somewhat higher level (section b), two lateral traces depart from the vascular cylinder, and slightly above (section c), the two median bundles branch out. At this point, the gaps of the laterals are closed again, and the sclerenchyma has formed a sickle-shaped sheath around them towards the outside, as well as a small strand between the bundles and the stele.

As we further approach the node, the vascular cylinders supplying the lateral shoots (L) can be seen departing from the stele (section d; not cut exactly at a right angle to the stem). It should be mentioned that at this stage the gamophyllous "Unterblätter" and the stem now have become two distinct units (sections d and e: dotted line). The leaf bases remain fused, although they also envelop the newly produced lateral shoots. The amount of sclerenchymatic tissue has increased in the stem: now there are two massive lateral strands plus four smaller ones.

A little higher (section e), the four traces of the "Unterblätter" can still be seen ascending in a vertical direction. There is, however, a first indication that the two lateral traces are beginning to split: the bundles which appeared as semicircles in sections c and d are starting to separate into two units. In section f (only fused leaf bases shown), finally, the two lateral bundles fork, with a portion moving toward each of the opposite median traces. Section g, cut slightly below the abscission layer, shows the lateral traces still passing through the leaf base toward the median bundle. They have forked again, and two small traces have entered the sides of the "vaginal lobe" (V). Slightly higher, section h cuts the base of the leaf blade (with the large median and the two circular lateral bundles), and the "vaginal lobe" (with two small lateral traces) and "stipules" (no vascularization), neither of which is any longer connected with the blade.

Within the leaf blade, the traces split up further. Normally, however, only the median bundles fork once or twice, while the lateral traces often remain unbranched (also see Grundell, 1933, *fig. 6*).

DISCUSSION

The Myrothamnaceae so far are the ninth family of dicotyledons with "split-laterals." It, however, appears to be the only family in which "split-laterals" are a family characteristic: preliminary investigations of herbarium material of *Myrothamnus moschatus* Baillon, the only other species of the genus (or of the family), yielded a vascularization pattern

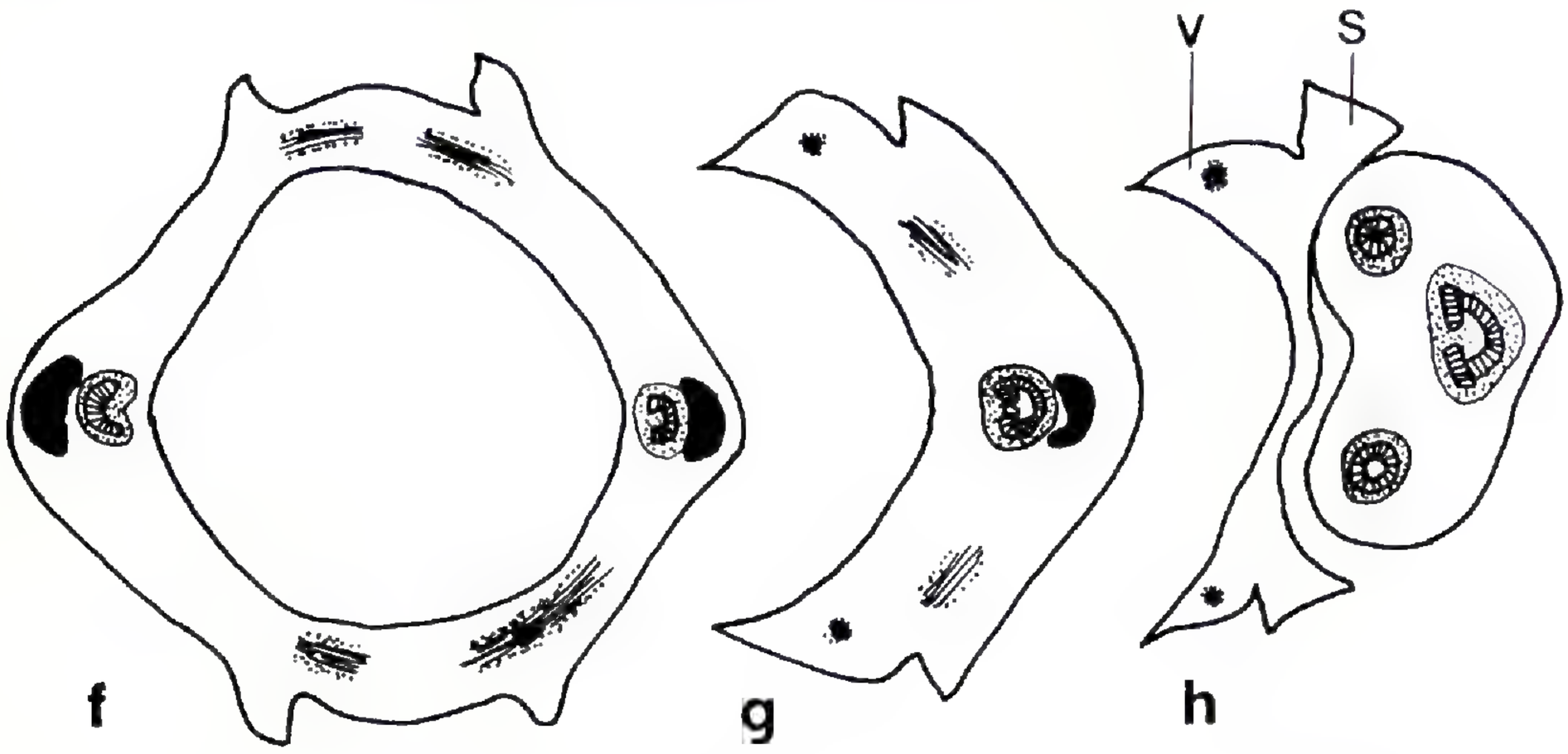


FIGURE 2. **Myrothamnus flabellifolius:** camera lucida drawings of sections through leaf bases. Black areas: sclerenchymatic tissue; hatched areas: xylem; dotted areas: phloem.

very similar to that of *M. flabellifolius*. More material, however, is needed to verify this.

Myrothamnus flabellifolius, like the other plants known to have split-lateral traces, has opposite (decussate) leaves and "stipules" or stipule-like processes[3] (for exceptions, see Howard, 1970). Unusual, and so far not known in plants with split-lateral bundles, however, are the gamophyllous "Unterblätter" of *M. flabellifolius*, which completely envelop the stem (and the bases of newly produced lateral shoots). In *M. flabellifolius*, the lateral bundles fork within the leaf (i.e., "Unterblatt"), and not, as in other plants with "split-laterals," in the stem (cortex): only after ascending vertically in the leaf base for a distance do they fork, pass around about a quarter of the "Unterblatt," and eventually join the median trace laterally (a "shift" of the "split-lateral" from the stem region to the leaf). As "stem" and "leaf," however, must developmentally and morphologically be considered a continuous system (see Howard, 1974), this peculiarity of *M. flabellifolius* appears to be of little significance.

PLANT MATERIAL EXAMINED

Southwest Africa (Namibia): Ameib farm near Usakos, on path to Phillips Cave, *Puff 760714–1/2*; Gamsberg pass, *Puff 760717–1/1* and *–2/1*.

South Africa. N. NATAL: Ngotoshe Dist., Ngome, near sawmill, *Puff 760610–5/1*. TRANSVAAL: Bosmanskop area near Badplaas, *Puff 770103–7/3*; Wolkberg area near Haenertsburg, *Puff 770108–5/2*.

Swaziland: Mdzimba Hills near Mbabane, *Puff 770119–1/1*; Lebombo Mts., Blue Jay Ranch, near Mozambique border, *Puff 770123–3/4*.

[3] In addition, it has "vaginal lobes." The true morphological nature of both "stipules" and "vaginal lobes" has yet to be clarified. An ontogenetic study could prove to be useful: according to Weberling (1975), true stipules always develop early and distinctly proleptically, whereas other appendages ("sheath lobes" of Weberling) develop at a later stage.

All specimens are deposited at the herbarium of the Institute of Botany, University of Vienna (WU).

Sections were cut freehand with a razorblade and stained in phloroglucinol and hydrochloric acid.

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COVER: The stylized representation of fruits of various Leguminosae, forming the design of our new cover for Volume 59, is based on material from plants growing in the Arnold Arboretum of Harvard University. The design was planned and executed by Karen S. Velmure, who has also drawn several of the preceding covers as well as various devices used in the *Journal of the Arnold Arboretum* and on the offprint covers.

The three subfamilies of the Leguminosae are represented by the fruits shown in the design. The genera are, top row (left to right), *Albizia* (Mimosoideae), *Gleditsia* (Caesalpinioideae), *Caragana* (Faboideae), *Gymnocladus* (Caesalpinioideae), and lower row, right, *Colutea* (Faboideae).

The family Leguminosae, the second most important family of flowering plants, is to be the subject of an International Legume Conference at the Royal Botanic Gardens, Kew, Richmond, Surrey, England, in July, 1978. This cover is our salute to the complete success of that Conference.

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JOURNAL
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THE GENERA OF CRASSULACEAE IN THE SOUTHEASTERN UNITED STATES [1]

STEPHEN A. SPONGBERG

CRASSULACEAE A. P. de Candolle in Lamarck & De Candolle, Fl. Franç. ed. 3. 4(1): 382. 1805, nom. cons.

(STONECROP or ORPINE FAMILY)

Annual, biennial, or [monocarpic or] polycarpic perennials, the plants mostly succulent, often evergreen, herbs, subshrubs [or shrubs, many of treelike habit, or rarely scandent], usually terrestrial from fibrous roots, sometimes developing fleshy or woody caudices or rhizomes [or rarely epiphytic]. Leaves exstipulate, alternate, opposite, or whorled, the internodes sometimes reduced and the plants rosulate, the blades simple or occasionally pinnately compound, usually fleshy and succulent, cylindrical to flattened with entire to crenate or dentate margins, the leaves of vegetative and flowering shoots often dissimilar; vegetative reproduction commonly by bulbil or plantlet production in the crenations of the leaves or by meristematic activity in detached leaves or stems. Flowers perfect or

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants of this area, with supplementary information in brackets. The literature listings given in this paper, although voluminous, are by no means all-inclusive, particularly for *Crassula* and *Kalanchoë*, and references that I have not seen are indicated by an asterisk.

I am most grateful to Professor Wood for his continued patience during the preparation of the manuscript, for his careful review of its content, and for help with numerous problems. I should also like to thank E. B. Schmidt for her careful editing. Figures 1 and 3 were prepared by Karen S. Velmure; Figure 2 was drawn by Rachel A. Wheeler. Living and alcohol-preserved plants used for the illustrations and for dissections were kindly supplied by R. C. Rollins, R. D. Thomas, R. E. Weaver, Jr., R. L. Wilbur, K. A. Wilson, and C. E. Wood, Jr.

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imperfect (the plants then dioecious or polygamodioecious), actinomorphic, usually proterandrous, arranged in terminal or axillary, usually bracteate corymbose, helicoid, or scorpioid cymes, panicles, simple to compound dichasia, or solitary [or clustered] in the axils of leaves [or rarely in spikes]; insertion of the sepals and petals hypogynous. Sepals (3) 4 or 5 [or up to 30], free or connate and then forming a calyx tube. Petals the same number as the sepals, free or occasionally connate, forming a tubular to urceolate, usually ribbed corolla tube. Stamens as many or twice as many (and then obdiplostemonous) as the sepals, insertion hypogynous or epipetalous, free [or occasionally the filaments basally connate]; anthers basifixed, dehiscing introrsely by longitudinal slits, 4-sporangiate (2-loculate at anthesis), with a secretory tapetum; pollen 2-celled when shed (as monads), 3-colporate. Gynoecium apocarpous or basally syncarpous, the carpels usually the same number as the sepals, sessile or stipitate, tapering gradually or abruptly into erect or divergent styles, the styles terminated by small, often poorly differentiated apical or subapical stigmas; each carpel subtended by a scalelike [rarely petaloid] nectariferous gland [or rarely, the gland absent]; ovary 1-loculate, superior, with numerous [rarely few to solitary] anatropous, crassinucellar, bitegmic ovules on a parietal or marginal placenta. Fruit a follicle or follicetum of several basally connate follicles, the follicles dehiscent along their adaxial sutures or rarely by abaxial flaplike valves; seeds usually numerous, small, rarely winged; embryo small, straight, embedded in scant, fleshy, cellular endosperm [or endosperm occasionally lacking]; megagametophyte of the Polygonum or (rarely) Allium type; embryogeny of the Caryophyllad type. (Sedaceae Necker, nom. subnud.) TYPE GENUS: *Crassula* L.

Upward of 1500 species in as many as thirty-five genera and six generally recognizable subfamilies, distributed throughout the world, primarily in areas of subtropical climate with alternating wet and dry seasons. Great concentrations of species and genera occur in southern Africa, Madagascar, the Canary Islands, southern Asia, Mexico, and the Mediterranean region. The family is poorly represented in Australia (one genus), Oceania (two genera) and South America. Nine or ten species in three genera (representing two subfamilies) are indigenous in the southeastern United States, while eleven or twelve additional species (eight of which represent a fourth genus and a third subfamily) have escaped from cultivation and have become naturalized in this area.

While the family Crassulaceae has generally been conceded to form a natural, well-defined taxon, agreement with regard to the definition of taxa at essentially all subordinate levels has been fraught with difficulties, and there is no general consensus as to the number of species, genera, or subfamilies. Berger (1930), who treated the entire family, recognized six subfamilies that, except for inevitable intermediate taxa, are fairly well defined morphologically, if not biologically. Baldwin (1939) suggested that the relationships within the family are interlinear as well as linear, and Berger (1930, p. 382) cautioned about the use of technical characters

in the definition of taxa. Berger's sentiments were reiterated by Moran (1942b), who said that "if too much emphasis were placed on technical characters, the numerous exceptions and intergradations would necessitate the combination of genera until but six or only one genus remained."

The characters that have been used to define subfamilies are largely concerned with the number of floral parts and the connation of the petals, as well as the position of the flowering shoots and the arrangement of the leaves. Certainly some of the problems below the level of subfamily are due to the usual succulence of the plants and the poor specimens that result from attempts to press the plants by conventional herbarium techniques. It is almost imperative that studies of the Crassulaceae be made with living plants or at least with fluid-preserved materials.

Members of the family are generally succulent and usually show a whole series of xeromorphic adaptations (including anatomical and physiological changes), as well as adaptations in the life cycles of some species (e.g., *Diamorpha Smallii*) for drought evasion. Most species have an abundance of water storage tissue in the leaves (in which a palisade layer is rarely or poorly differentiated) and in the stems (where the parenchymatous or collenchymatous tissues of the cortex and pith are well developed). Vascular tissue is unevenly and irregularly distributed throughout the storage tissues, the phloem is poorly developed, and the xylem of the stems is generally in a continuous cylinder.

While trichomes are uncommon in the family, the hairs (as well as the adventitious roots and epidermal cells) of some species are suspected of absorbing water directly from the atmosphere. A waxy coating secreted by the epidermis is characteristic of the leaves, and hydathodes are relatively common, often being distributed over both surfaces of the leaves and visible to the naked eye as small pits. The stomata, which are usually surrounded by three subsidiary cells, are likewise usually well distributed over both surfaces of the leaves.

The stomata of some investigated species are open primarily at night and closed during the day, a phenomenon that coincides with carbohydrate decrease, excessive increase in malic acid content, and water-vapor loss at night, and with starch accumulation and reduced acidity during the daylight hours. Carbon fixation occurs in the leaves at night when the stomata are open, and is thus temporally separated from the light reactions in the photosynthetic process. During the day, when the stomata are closed and water loss is thus reduced, the fixed carbon is reduced to carbohydrate. This physiological syndrome, known as crassulacean acid metabolism (CAM), along with the Calvin-Benson cycle (C_3 plants) and the C_4 decarboxylic pathway (C_4 plants), is one of three distinct carbon fixation and reduction mechanisms known in vascular plants. While the CAM pathway was originally described from crassulaceous plants, it is not restricted to them, and it may be facultative, depending upon environmental conditions. Kluge (1977) has found that under normal conditions in nature, *Sedum acre* is a C_3 plant, but that under experimental water stress, carbon dioxide exchange shifts from the Calvin cycle to CAM. As

indicated by Black & Williams (1976), all CAM plants are succulents, but not all succulents are CAM plants. Apparently there is little if any taxonomic significance to CAM, since the pathway has been reported for members of four monocotyledonous and thirteen dicotyledonous families, as well as for a fern, *Drymoglossum piloselloides*. While only the outlines of the process are given above, there has been much research on CAM; for further information, see the papers listed under family references, as well as a few titles included under *Kalanchoë*.

Other features of the Crassulaceae of biological interest are the wide range of chromosome numbers (from $2n = 8$ to $2n =$ ca. 500) and the occurrence of considerable and widespread intraspecific variation in chromosome number, including both polyploidy and aneuploidy. Uhl (1970) reports that two species of *Graptopetalum* Rose have gametic chromosome numbers of $n = 245 \pm 5$ and $n = 270 \pm 5$, higher counts than have been reported for any other seed plants. The occurrence of heteroploidy has proved to be confusing, particularly with regard to species delimitation, and especially when few if any morphological characters correlate with the different chromosome numbers.

Uhl (1976) has determined that the majority of the Crassulaceae of Mexico (subfams. Sedoideae and Echeverioideae) ". . . belong to a giant biosystematic comparium, since they have been interconnected, directly or indirectly, by artificial hybrids. More than 1100 different hybrids have been produced among at least 165 species of the genera *Echeveria*, *Sedum*, *Pachyphytum*, *Graptopetalum*, *Thompsonella*, *Villadia*, and *Lenophyllum* . . . ." Moreover, the intersubfamilial hybrid between *Echeveria linguifolia* Lemaire and *Sedum cremnophila* Clausen, both with $2n = 66$, has normal meiosis and 95 percent normal pollen (Uhl, 1966, 1976). It would appear that continued chromosome studies, together with hybridization programs, in other groups of the family will alter the concept of relationships at almost all ranks and will undoubtedly provide the basis for a more acceptable (if not a more utilitarian) taxonomy.

In current systems of classification, the Crassulaceae are closely allied with the Saxifragaceae, from which they can be distinguished by their usual succulence and their flowers with the number of petals or sepals and carpels the same, the carpels subtended by nectariferous glandular scales, and the seeds lacking (or with only scant) endosperm. *Penthorum* L. is the only genus that has created problems in the delimitation of the Crassulaceae, and Quimby (1971) has concluded that this family is a natural assemblage only if *Penthorum* is excluded. Although *Penthorum* exhibits characters that are in many respects intermediate between the two families (it has occasionally been placed in its own monogeneric family, Penthoraceae Rydb. ex Britton), in this flora *Penthorum* has been included in the Saxifragaceae in subfam. Penthoroideae Engler, for the reasons outlined there (Spongberg, 1972, p. 421).

Thorne (1968) and Cronquist (1968) include Crassulaceae and Saxifragaceae in the Rosales, while Takhtajan (1969) includes the two families in the Saxifragales. Both Takhtajan and Cronquist note that the Podo-

stemales (Podostemaceae) (included in the Rosales by Thorne) are undoubtedly derived from the Crassulaceae. Support for a close relationship between the Crassulaceae and the Podostemaceae, seemingly dissociative taxa, comes primarily from embryological similarities noted by Mauritzon (1939), Maheshwari (1945), and Subramanyam (1962) that have been summarized in this flora by Graham & Wood (1975). An evolutionary trend toward adaptation to an aquatic habitat is also evident in the Crassulaceae in some members of *Crassula* sect. TILLAEOIDEAE.

None of the Crassulaceae is of great economic importance, although many of the species are cultivated as ornamentals, both as pot plants and as garden perennials. In our area, species of *Sedum* and *Sempervivum* (subfam. Sempervivoideae Berger) are commonly grown in rock gardens and on walls. Some of the species have been used in folk medicine and as greens in salads.

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KEY TO THE GENERA OF CRASSULACEAE IN THE SOUTHEASTERN UNITED STATES

A. Petals (3) 4 or 5, free or only slightly connate at base; stamens free from the petals and inserted hypogynously.
  B. Stamens 2× the number of sepals and petals (subfam. Sedoideae).
    C. Gynoecium apocarpous; flowers perfect or imperfect, 4- or 5-merous; mature follicles dehiscing longitudinally; annuals, biennials, or perennials. ..... 1. *Sedum.*
    C. Gynoecium syncarpous at base; flowers perfect, 4-merous; mature follicles dehiscing by a tear-shaped, flaplike, abaxial valve; winter annuals. ..... 2. *Diamorpha.*
  B. Stamens the same number, (3) 4, as the sepals and petals; gynoecium apocarpous; mature follicles dehiscing longitudinally along the adaxial suture; annuals or biennials (subfam. Crassuloideae). .... 3. *Crassula.*
A. Petals 4, connate; stamens 8 (in 2 whorls of 4), epipetalous; gynoecium basally syncarpous; perennials naturalized in southern Florida (subfam. Kalanchoideae). ..... 4. *Kalanchoë.*

Subfam. SEDOIDEAE Berger

1. **Sedum** Linnaeus, Sp. Pl. 1: 430. 1753; Gen. Pl. ed. 5. 197. 1754.

Annual, biennial, or perennial, ± succulent, often evergreen or deciduous herbs [subshrubs or shrubs], cespitose or with mat-forming vegetative shoots and then usually with slender, ascending or erect, terminal or occasionally axillary flowering stems. Roots generally fibrous, occasionally thick and tuberous, sometimes from a rhizome or a fleshy or woody caudex. Leaves glabrous, often glaucous [or rarely glandular-pubescent], mostly alternate, occasionally opposite or whorled, often imbricate and sometimes subrosulate, sessile or short-petiolate, often spurred at base, the blades flattened to cylindrical, ovoid, or subglobose, when flattened, linear to lanceolate, oblanceolate, ovate, or suborbicular in outline with entire to dentate margins [rarely spine-tipped]; leaves of vegetative and flowering

shoots often dissimilar. Flowers perfect or imperfect (and the plants then dioecious or polygamodioecious), arranged in axillary or terminal, often bracteate, diffuse to compact corymbose, helicoid or scorpioid cymes (often with several helicoid or scorpioid cymes terminating a single flowering stem), in simple or compound dichasia [or rarely solitary or in spikes]; insertion of the floral parts hypogynous. Sepals 4 or 5 [or rarely up to 9], imbricate or valvate in bud, free or connate basally, often fleshy and bractlike or leaflike. Petals 4 or 5 [or as many as the sepals, or sometimes absent in carpellate flowers of dioecious species], free or slightly united basally, erect or patent, yellow, greenish, white, pinkish, purplish [or very rarely blue], usually narrowly elliptic or subulate in outline, sometimes keeled. Stamens 8 or 10 [or twice the number of sepals] in 1 or 2 whorls, free [or those opposite the petals occasionally epipetalous]; filaments subulate to filiform, tapering to the yellowish or reddish anthers. Gynoecium of 4 or 5 [or as many as the number of sepals] erect or divergent carpels, the carpels free [or only slightly coherent basally], tapering into short, slender styles above; ovaries unilocular, with numerous [or rarely 1 or few] ovules on 2-lobed parietal placentae along the adaxial sutures. Fruits erect or divergent follicles, often with stylar beaks, with many [or rarely 1 or few] seeds, dehiscent along the adaxial sutures; seeds usually small, sometimes winged, with fleshy endosperm surrounding the straight embryo; megagametophyte of the Polygonum or Allium type. Base chromosome numbers 4, 5, 6, 7, 8, 9, 10, 11. (Including *Anacampseros* Haw., *Hylotelephium* H. Ohba, *Rhodiola* L., *Tetrorum* Rose.) LECTOTYPE SPECIES: *S. acre* L.; see Hitchcock, Prop. Brit. Bot. 156. 1929. (Name from Latin, *sedere*, to sit or hold fast, in reference to the manner in which numerous species grow on rock outcrops and on walls; said by some to be derived from Latin for to assuage or soothe, apparently in reference to their reputed healing qualities.) — STONECROP, LIVE-FOREVER, ORPINE.

A large genus of some 300 to 600 species (Willis, 1966) widely distributed in the Temperate Zone of the Northern Hemisphere, extending into the Arctic (ca. four species), and into the Southern Hemisphere of the Old World in the equatorial mountains of East Africa and in Madagascar. In the Western Hemisphere species of the genus range into South America in the Andes of Bolivia and Peru. Great concentrations of species are found in western North America; in Mexico, where twenty-eight species are endemic to the trans-Mexican volcanic belt alone (Clausen, 1959); in Europe and the Mediterranean region; and in eastern Asia. In the southeastern United States seven or eight species are native, while three or four additional taxa have been reported as escapes from cultivation. Clausen (1975) recognized twenty-two additional species as native to North America north of the Mexican Plateau, and he also recorded thirteen (both native North American and exotic) taxa as naturalized, while he included fifty-three species in his annotated list of cultivated species.

Largely in response to interest in the species as garden plants, the first modern treatment of *Sedum* was prepared by Praeger (1921), who, in

accounting primarily for taxa known in cultivation, laid the basic taxonomic framework for the genus. Praeger distributed the species among ten sections and numerous groups, while Berger (1930), treating the entire genus, recognized twenty-two sections, as well as subordinate series and groups. Fröderström (1930, 1931, 1932, 1935), who prepared the most exhaustive world-wide treatment, recognized two sections (RHODIOLA and TELEPHIUM) but treated the remaining species on a geographic basis, dividing taxa within each major geographic area into two classes (on the basis of erect versus divergent carpels) and numerous subordinate groups. In Praeger's and Berger's classifications, which are generally more utilitarian, are currently in wider use, and also coincide at the sectional rank for our species, the native and adventive southeastern species belong to four sections. In treating the North American species, Clausen (1975) has recognized three of these four subgeneric taxa but has elevated each of them to the rank of subgenus while including the species of the fourth, sect. EPETEIUM Boiss., in subg. SEDUM. He recognizes five sections within subg. SEDUM and two within subg. RHODIOLA.[2]

Section RHODIOLA (L.) Scopoli (*Rhodiola* L., pro gen., *Sedum* subg. *Rhodiola* (L.) H. Ohba) (perennials with deeply rooted, fleshy or woody caudices terminated by clasping, well-developed or reduced, scalelike leaves with annual, leafy flowering stems developed in their axils, the mature follicles erect, with stout stylar beaks) is primarily a Eurasian group that is represented in North America by only two (or perhaps three) species. *Sedum Rosea* (L.) Scopoli (*Rhodiola Rosea* L., *Sedum Rhodiola* DC., *S. roanensis* Britton, *S. Rosea* var. *roanensis* (Britton) Berger, *Rhodiola roanensis* (Britton) Britton), $2n = 18, 22, 32, 33, 36$, is a wide-ranging circumpolar species, with a discontinous distribution at higher altitudes in mountainous regions, that occurs throughout much of Asia, northern Europe, and arctic and boreal North America. In our area, it has been recorded from over 6,000 feet on Grandfather Mountain, North Carolina, and on Roan Mountain, on the North Carolina-Tennessee boundary. These southern localities, where *S. Rosea* grows in moist soil in crevices and on rock ledges, usually on north-facing cliffs, are some 500 miles south of the nearest known populations in Bucks County, Pennsylvania. Farther north it occurs at high elevations in New York, Vermont, and northward along the coast of Maine into Canada. In western North America, *S. Rosea* extends southward in the Cordillera into California, Colorado, and New Mexico, and in the Rocky Mountains (where it is sometimes segregated as *S. integrifolium* (Raf.) A. Nelson (*Rhodiola integrifolia* Raf., *S. Rhodiola* Torrey, not DC.) or treated as *S. Rosea* subsp. *integrifolium* (Raf.) Hultén), it is often sympatric with *S. rhodanthum* A. Gray (*Clementsia rhodantha* (A. Gray) Rose), $2n = 14$, the second representative of the section in North America.

[2] Although Clausen (1975, p. 474) proposed *Sedum* subg. RHODIOLA, the change in status had been proposed by H. Ohba (1975, p. 285) some months before the publication of Clausen's treatment. Despite this, Ohba (1977) credits the combination to Clausen.

Characterized by usually imperfect, four-merous flowers in dense, terminal corymbose cymes and by fleshy or woody caudices that reputedly emit an odor of roses when dried, plants of *Sedum Rosea* are dioecious or occasionally polygamodioecious; individuals and entire populations with perfect flowers occur in some areas. The petals are greenish or yellowish, often tinged red at the apex, or deep red, and the numerous, closely spaced, glaucous, alternate leaves of the erect stems are oblanceolate, with acute apices and entire or irregularly dentate margins.

Extremely polymorphic over its wide geographic range, *Sedum Rosea* consists of numerous races that differ from one another primarily in flower color, leaf-margin dentation, and plant size and habit. Numerous segregate taxa have been proposed, particularly from Asia. Britton & Rose (1903, 1905) considered the southern Appalachian populations to comprise a distinct species (*S. roanensis*, as a species of *Rhodiola*); they also recognized four segregate species in western North America. Hultén (1945), however, contended that the majority of segregate taxa should be considered informally as local races, while others should, at most, be treated at the subspecific or varietal rank.

Sedum Rosea is also variable cytologically, and Uhl (1952) has shown that two chromosome races, one with $2n = 22$, the other with $2n = 36$, are widespread in North America. Wiens & Halleck (1962), however, have reported that Rocky Mountain plants of *S. Rosea* have $2n = 32$, and a count of $2n = 18$ has been reported by Sokolovskaya & Strelkova (1960). Other than inconsistent differences in flower color, plant sexuality, and habit, the cytological differences appear to lack morphological correlations, yet the 22-chromosome race occurs in glaciated northeastern North America (and in Eurasia), while the 36-chromosome race is apparently confined to unglaciated areas of the continent. Plants from our area remain uninvestigated cytologically, and, although it has been questioned whether these southern populations are still extant (Wherry, 1934; Uhl, 1952), Clausen (1975) reported seeing two plants on Roan Mountain in 1972.

Section TELEPHIUM S. F. Gray (*Sedum* subg. *Telephium* (S. F. Gray) R. T. Clausen, *Hylotelephium* H. Ohba) (perennials from caudices lacking scalelike leaves, with slender to thick fusiform roots, producing erect, rarely decumbent, usually annual, leafy flowering stems; flowers perfect, 5-merous, with erect, stipitate carpels, the mature follicles erect, with slender stylar beaks) is also widely distributed in temperate regions of Eurasia and is represented in our flora by *Sedum telephioides* Michaux (*Anacampseros telephioides* (Michaux) Haw., *Hylotelephium telephioides* (Michaux) H. Ohba), $2n = 24$. The only species of the section indigenous to North America, *S. telephioides* grows on rock ledges and in crevices on exposed and shaded cliffs, and on stony slopes in rich woods in the mountains and adjacent upper Piedmont from southern Pennsylvania southward into Georgia; it is also known from limestone bluffs along the Ohio River in southern Indiana (Harrison County) and from southern Illinois.[3]

[3] House (Annot. List Pl. N. Y. 376. 1924) pointed out that records for *S. tele-*

Blooming in late summer and fall, *Sedum telephioides* is rather variable vegetatively but is easily recognized among our native sedums by its erect stems with flattened, mostly alternate or sometimes opposite, occasionally glaucous, broadly ovate leaves with subentire to coarsely toothed margins, and its numerous flowers arranged in corymbiform cymose inflorescences 2.5–8(–14) cm. broad. The carpels are pinkish, subtended by nectariferous scales about as broad as long, and the sepals and stamens are shorter than the pink to whitish petals.

Closely allied to *Sedum Telephium* L., a wide-ranging Eurasian species, and the numerous (up to 25) additional Eurasian taxa included within this complex (several of which have been variously either segregated from or included within *S. Telephium*), S. *telephioides* has been retained as a distinct species by American botanists despite the suggestions of both Praeger and Berger that it is probably only a variety of *S. Telephium*. Like the *S. Rosea* group, the *S. Telephium* complex is exceedingly variable both morphologically and cytologically, and its classification and nomenclature are both confusing and in need of careful study. As a group, the Eurasian taxa can reputedly be distinguished from *S. telephioides* by their fusiform roots, their flowers with the sepals scarcely one-third as long as the petals, their stamens about equaling or exceeding the petals, and their nectariferous scales longer than broad.

Of the taxa included within the *Sedum Telephium* group, *S. telephioides* appears to be most closely allied to *S. Telephium* subsp. *alboroseum* (Baker) Fröd. (*S. erythrostictum* Miquel, *S. alboroseum* Baker, including *S. spectabile* Boreau, *fide* Fröderström, *Hylotelephium erythrostictum* (Miq.) H. Ohba), $2n = 48, 50, 51$, of China, Manchuria, and Japan, which has been reported as an escape from gardens in northeastern North America, southward into Virginia and North Carolina. An herbaceous perennial with spreading to procumbent stems to 60 cm. tall, with alternate, opposite, or whorled leaves and pinkish white flowers in flat corymbose cymes, subsp. *alboroseum* flowers in late summer and fall and is also closely linked to *S. Telephium* subsp. *Telephium* var. *purpureum* L. (*S. Telephium* subsp. *purpurascens* (Koch) Areschoug, *S. purpureum* (L.) Schultes, *S. purpurascens* W. D. J. Koch), $2n = 36, 48$.[4] Also a common garden plant, *S. Telephium* var. *purpureum* has been reported as an escape and persisting outside of cultivation near waste heaps in Warren County, North Carolina. Native to Europe, plants of *S. Telephium* var. *purpureum* are stout, glabrous herbs from fusiform roots, with alternate, broadly oblong or elliptic leaves with coarsely and irregularly toothed margins and flowers with purplish red to rosy petals in dense, terminal and lateral, subglobose cymes. Unlike those of *S. telephioides*, the leaves of *S. Telephium* var.

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phioides from western and central New York state are generally attributable to *S. Rosea*. One substantiated report from Dutchess County is probably based on a plant escaped from cultivation (cf. Wherry, 1936).

[4] Material determined to be $2n = 48$ tentatively assigned to subsp. *Telephium* var. *purpureum* (as subsp. *purpurascens* (Koch) Areschoug) by Jalas & Rönkkö (1960).

purpureum are reduced in size up the flowering stems. *Sedum Telephium* has also been listed as persisting outside of cultivation in Knox and Sevier counties, Tennessee, but it is not known to which subspecies these plants should be assigned. Allard (1932, 1940), moreover, contended that true *S. Telephium* is a long-day plant that rarely blooms in gardens south of New England. It is obvious that the reports of taxa of this complex in our area should be examined critically during the course of an overall study of the group.

The majority of species of *Sedum* have been placed in sect. SEDUM (*Seda Genuina* W. D. J. Koch, sect. *Eusedum* Boiss., subg. *Sedum* fide R. T. Clausen) (annual or usually perennial herbs or subshrubs with creeping rhizomes, cespitose sterile stems, and erect or ascending flowering stems; flowers perfect, the mature follicles divergent). This section is represented in the southeastern states by four native species and two adventives that have become naturalized.

Sedum pulchellum Michaux (including *S. vigilmontis* Small), $2n = 22$, 44, 66, occurs primarily on limestone, but also grows on granitic and siliceous outcrops in open and wooded habitats from western Virginia through Kentucky and Tennessee to southern Illinois, Missouri, and Kansas, and southward into northwestern Georgia, northern Alabama, Arkansas, Oklahoma, and Texas. *Sedum pulchellum* is usually a winter annual or occasionally a biennial or perennial due to persistence of vegetative shoots. Its seeds germinate in the fall and produce small, lax rosettes of flat, greenish gray, oblong-spatulate leaves (FIGURE 1, a). Early in spring, decidedly different erect flowering stems develop with narrowly linear, cylindrical, terete leaves with auriculate or sagittate bases (FIGURE 1, b). These leafy stems, 10–30 cm. high, are terminated by three (rarely to seven) widely divergent, recurved, secund scorpioid cymes 3–4 cm. long comprising many four-merous flowers with whitish to deep pink or purplish petals that are about twice as long as the small sepals.

In their vegetative, over-wintering stage, plants of *Sedum pulchellum* have been confused with *S. Nevii* A. Gray (*S. Beyrichianum* Masters (?), *S. Nevii* var. *Beyrichianum* (Masters) Praeger (?)), $2n = 12$, a narrow endemic known with certainty from only five localities (three in Alabama, one in southeastern Tennessee, and one in extreme west-central Georgia near the Alabama line). A slender, only slightly glaucous perennial with loose, sterile rosettes of leaves 1–5 mm. wide, flowering stems with 12–40 narrowly oblanceolate or linear-oblanceolate, usually subterete leaves 3–19 mm. long, 1–3 mm. wide, white, four-merous flowers in two or three slender helicoid cymes terminating flowering stems, and seeds 0.5–0.6 mm. long, *S. Nevii* grows on exposed and/or shaded cliffs and rock ledges. Until Baldwin's (1942) cytological investigations revealed that the Alabama plants are diploids with $2n = 12$, it was generally assumed that *S. Nevii* had a wider range in the eastern United States. Virginia plants referred to *S. Nevii*, however, proved to be diploids with $2n = 28$, and, as a result of this chromosomal difference and very subtle morphological dissimilarities, Clausen (1946) segregated the Virginia populations as *S. glaucophyllum*.

FIGURE 1. **Sedum**. a–d, *S. pulchellum*: a, over-wintering rosette, × ½; b, flowering shoot, × 1; c, flower, × 5; d, cross section through four carpels of gynoecium, × 20. e–j, *S. pusillum*: e, habit of mature plant, × 1; f, longitudinal section through immature follicles (note nectaries, solid black, at base of carpels), × 6; g, immature follicles, × 6; h, mature, dehisced follicles, × 6; i, seed, × 25; j, embryo, × 25. k, *S. glaucophyllum*, leafy shoot, × 1. l, *S. ternatum*, leafy shoot, × ½. m, *S. telephioides*, outline of leaf, × ½.

Moreover, western records for *S. Nevii* in southern Illinois and Missouri have resulted from confusion with *S. pulchellum* (cf. Wherry, 1934, 1936).

Further cytological investigations by Uhl (1970) have revealed chromosome numbers of $2n = 28$, 44, and 56 within *Sedum glaucophyllum*, which is now known to range from southern Maryland, southward through the mountains and adjacent Piedmont of West Virginia, Virginia, and North Carolina, where it is known from Rockingham and Surrey counties. A

glaucous perennial with dense, sterile rosettes of leaves 2–7 mm. wide, flowering stems with 30–50 flat, oblanceolate leaves 5–25 mm. long and 2–6 mm. wide, white, four-merous flowers in three or sometimes four slender helicoid cymes terminating the flowering stems, and seeds 0.5–0.9 mm. long, *S. glaucophyllum* grows in moist rock crevices on both sunny and shaded cliffs.

Acceptance of the distinct species status of *Sedum glaucophyllum* has been tentative since morphologically it is practically indistinguishable from *S. Nevii*, and the characters used to separate it are largely qualitative. Clausen himself (1946) cautioned that ". . . if the morphological and cytological differences are not correlated . . . the classification again must be revised and *S. glaucophyllum*, though a genetical species, would need to be handled taxonomically as a synonym under *S. Nevii*, since it would not be a practical unit capable of recognition by ordinary observation." However, since *S. Nevii* sensu stricto is a narrowly restricted endemic, the use of the name *S. glaucophyllum* for plants throughout the distinct, more northeastern range of that taxon is facilitated on a geographic basis and seems justified considering the state of our biological knowledge of both taxa.

Another species of sect. SEDUM, *Sedum ternatum* Michaux (*Anacampseros ternata* (Michaux) Haw.), $2n = 16, 24, 32, 48$, is widely distributed throughout the eastern United States, from New Jersey and Pennsylvania, west through Ohio and Illinois to Missouri, and southward to the Carolinas, Georgia, and Arkansas. Easily recognized by its flat, elliptic to spatulate or rounded leaves usually in whorls of three on sterile shoots, and its obovate to spatulate leaves on the erect flowering stems, *S. ternatum* is a procumbent, mat-forming perennial with white, four-merous flowers with crimson or purplish anthers. The flowers are usually arranged in three terminal scorpioid cymes. The plant often occupies rich, moist sites in woodlands and frequently grows on rocky slopes and along stream banks where it sometimes forms extensive, carpet-like stands. Baldwin (1942) discovered the existence of four chromosome races: diploids ($2n = 16$), triploids ($2n = 24$), tetraploids ($2n = 32$), and hexaploids ($2n = 48$). While these races lack morphological correlations, the diploid race (West Virginia, Kentucky, and Virginia) and the hexaploid (one locality near Tuscaloosa, Alabama) have limited geographic ranges in contrast to the widespread tetraploid and the sporadic occurrence of triploid plants.

Sedum sarmentosum Bunge, a native of northern China and Japan, is also a prostrate, mat-forming perennial with long, creeping sterile shoots with leaves in whorls of three and erect flowering stems. Its flowers, however, are arranged in terminal compound cymes and are bright yellow. Occasionally cultivated as an ornamental, *S. sarmentosum* has been reported as naturalized in a few dry, open, rocky areas in the mountains of North Carolina. Small (1933, p. 588) probably confused this species with *S. mexicanum* Britton (*S. sarmentosum* Masters, not Bunge) when he said that it (*S. mexicanum*) ". . . is often cultivated and occasionally escapes from gardens" in the Southeastern States.

Another adventive, *Sedum acre* L., $2n = 16, 40, 48, 60, 80, 100, 120$, is native to a wide area of the Old World in Europe, northern Asia and Asia Minor, and northern Africa. Plants of this species are small, creeping, mat-forming, evergreen perennials, with bright yellow flowers produced in two or three terminal cymes. They can be recognized by the overlapping, alternate, flattish, deltoid leaves that are broad and slightly spurred at the base. One of the most widely cultivated sedums in rockeries and on walls, *S. acre* has apparently become naturalized in Avery and Mitchell counties, North Carolina.

Section EPETEIUM Boiss. (sect. *Procrassula* (Griseb.) Schönl., *pro parte*; *Procrassula* Griseb.) (annual or biennial herbs with slender, poorly developed root systems, the flowering plants lacking sterile shoots, with alternate, flattened or cylindrical leaves and branched cymose, corymbiform, or dichasial inflorescences comprising several to numerous 4–9-, mostly 5-merous flowers with white, yellow, red, or blue petals) is sometimes included within sect. SEDUM and is represented in our area by two species. *Sedum pusillum* Michaux (*Tetrorum pusillum* (Michaux) Rose), $2n = 8$, is a diminutive winter annual endemic to the Piedmont of the Carolinas and Georgia. In this region *S. pusillum* is totally restricted to granitic flat-rock communities, and it is sometimes confused with *Diamorpha Smallii* Britton (q.v.). *Sedum pusillum* is typically found growing in the partial shade of pines or *Juniperus virginiana* L. at the margins of the rock outcrops and in sheltered depression pits on outcrop surfaces, often near vernal pools. *Diamorpha Smallii*, on the other hand, grows in exposed depression pits with very shallow soils. A small, early-spring-flowering, usually branched herb 4–12 cm. high with bluish green (or sometimes reddish) cylindrical leaves and four- or rarely five-merous white or pinkish flowers with red anthers arranged in small helicoid cymes or simple or compound dichasia, *S. pusillum* differs in several significant anatomical and morphological features from *Diamorpha*. These differences, several of which are diagnostic in the field, are discussed under *Diamorpha*. The diploid chromosome complement of $2n = 8$ known for *S. pusillum* is the lowest diploid number recorded in the Crassulaceae (Baldwin, 1940).

Sedum Nuttallianum Raf. (*S. Torreyi* G. Don, *S. sparsiflorum* Nutt. in Torrey & Gray), $2n = 20$, also a diminutive winter annual, ranges from Arkansas and Missouri, southward into Oklahoma and Texas. Flowering from April to July, *S. Nuttallianum* grows in the shallow soils of chert and sandstone glades and ledges and in the clayey soils of pasturelands. Individuals of *S. Nuttallianum* are small plants 5–15 cm. high, usually branched from the base, with short, pale, silvery green, cylindrical, alternate leaves and sessile or short-pedicellate, five-merous flowers with lanceolate yellow petals arranged in two to five terminal cymes. Although the individuals are small, the plants commonly grow in large, dense populations and give an overall effect in the field of a low, mat-forming perennial.

Despite continued investigations of the genus, *Sedum* remains extremely

complex taxonomically and confusing nomenclaturally. While the subgeneric classification is not without problems, particularly some concerning the limits and validity or potential generic status of certain sections, the greatest confusion appears to center around the definition of species and subspecific taxa. Certainly some of the confusion is the result of the fact that "dried specimens can be the source of erroneous impressions concerning the dimensions and shapes of structures, as well as the habits of plants . . ." (Clausen, 1959, p. 337). In addition, many species are narrow endemics, while others are extremely wide-ranging and exhibit a polymorphism that appears to be proportional to the extent of the geographic range. Furthermore, individuals of a given taxon may appear quite different from one another depending upon their habitats and the time of year the plants are observed or collected. The color of the stems and foliage, for example, is prone to change, usually becoming reddish under dry conditions, with age, or when grown in intense light.

But, as pointed out by Uhl (1961), "the most conspicuous problem is the frequency with which heteroploidy occurs within what many authors have regarded as a single species. . . ." While this phenomenon is characteristic of the Crassulaceae in general, it is particularly evident in *Sedum*, where both polyploidy and aneuploidy have been documented for numerous species, several of which are native to our area. Furthermore, every gametic chromosome number from $n = 4$ to $n = 38$ is known in the genus. However, *S. spathulifolium* W. J. Hooker, $2n = 30$, is cited as an exception to the rule, inasmuch as it is a wide-ranging species (Vancouver Island, south to southern California) that apparently has the same chromosome number over its entire area (Uhl, 1961b).

As a possible explanation of the usual lack of morphological correlation with the heteroploid cytological condition found in numerous species, Uhl (1961b) suggests that these taxa are presently undergoing rapid evolution and that "each karyotype has not yet evolved its own distinctive genotype and phenotype. . . ." This hypothesis gains support from the fact that the usual habitats of species of *Sedum* are cliffs and rock outcrops, habitats that are discontinuous and unstable in terms of geologic time and, as a result, are probably conducive to rapid evolutionary rates. Likewise, Clausen (1959) suggests that the morphological and physiological differences between the closely related species endemic to the trans-Mexican volcanic belt are largely due to gene mutations, while changes involving chromosome number have led primarily to genetic isolation between sympatric taxa. Investigations employing electrophoretic techniques might give support to these interpretations.

While the chromosomes of *Sedum* are generally small, Uhl (1961) and Uhl & Moran (1972) point out that they seem to possess localized kinetochores, ruling out the possibility that the heteroploid condition is the result of diffuse kinetochores and chromosome breakage like that documented for *Carex* (Cyperaceae) (Davies, 1956). Levan (1933) reported heteromorphic sex chromosomes for a single plant of *S. Rosea*

from a dioecious population, but in his 1952 report, Uhl could not distinguish specific sex chromosomes.

In their cytological survey of Japanese and South Korean Crassulaceae, Uhl & Moran (1972) calculated the approximate nuclear volume of cells of taxa within two complexes of *Sedum*. A nearly proportional increase of nuclear volume was found in sect. AIZOON, a complex comprising diploids (where $n = 16$) to apparent heptaploids, suggesting that the change in chromosome number within this group is the result of "multiplication of the more or less complete genome." This situation is in contrast to that encountered in *S. polytrichoides* Hemsley ex Hemsley & Forbes, *sensu lato*, where no clear relationship between chromosome number and nuclear volume was evident. Uhl & Moran speculate that in this highly dysploid species, where plants are known to vary from $n = 11$ to $n = 35$, "very extensive rearrangement and repackaging of essentially the same amount and kind of chromosomal material, probably chiefly by translocations, have accompanied and made possible the many changes in chromosome number in this complex."

Interspecific hybridization, except within sect. TELEPHIUM, is thought not to occur in nature, and there have been no attempts to produce artificial hybrids utilizing cultivated materials (Evans, 1971). Even within taxa exhibiting polyploidy it has generally been concluded that the polyploid condition has been achieved through autopolyploidy and not through allopolyploidy. Certain hypotheses concerning the origins of some taxa, however, have been advanced that are based on the assumption that interspecific hybridization has occurred. Notable among these hypotheses is Baldwin's (1940) suggestion that *Diamorpha Smallii*, $2n = 18$, is the amphidiploid product of "fusions between the 4- and 5-chromosome tendencies" within *Sedum* as represented by *S. pusillum* and *S. Nuttallianum*, respectively.

The scant data concerning floral biology of *Sedum* indicate that there is a range from proterogyny and homogamy to marked proterandry. In proterandrous flowers the anthers of the outer whorl of stamens dehisce first, followed by the slightly delayed dehiscence of the anthers of the inner whorl. The movement of the stamens to an erect position over the carpels just before dehiscence and their subsequent return to the periphery of the flower afterward are suggestive of similar movements observed in flowers of several genera of subfam. Saxifragoideae of the Saxifragaceae. Although the maturation and receptiveness of the stigmas and the dehiscence of the anthers are usually not synchronous, self-pollination may occasionally occur; however, no studies have been located that deal with compatibility systems within the genus.

Nectar is secreted by the small, scalelike glands that subtend the carpels (the glands considered to be dorsal outgrowths of the carpels), and the few recorded observations suggest that visitors attracted to the flowers are usually dipterans, hymenopterans, and lepidopterans.

Dispersal of seeds from the mature, dehisced follicles is probably by wind action that sets up short-term vibrations of the follicles. The seeds

are small, and those of *Sedum Rosea* are narrowly winged at each end. The low, often creeping, vegetative shoots of numerous species root at the nodes, and propagation and dispersal undoubtedly occur frequently by vegetative means. Both pieces of stem and individual detached leaves of most species develop adventitious roots and shoots, and Yarbrough (1936) found that in leaves the mode of origin of these structures is through the activity of a secondary meristem that develops from vacuolated, differentiated parenchyma. This "regeneration" is in contrast to the formation of the plantlets produced along the leaf margins or at leaf or petiole bases in species of *Kalanchoë*, which are the result of the activity of a residual primary meristem.

The vascular anatomy of the flowers of a relatively large number of species was investigated by Quimby (1971), who placed these taxa in four groups based on the number of whorls of traces supplying the flowers. The majority of species (37) have four whorls of traces (Group III), while others have six (Group I, the presumed underived condition found in species of sect. TELEPHIUM), five (Group II), or three (Group IV) whorls. Vertical compression of the receptacle has apparently led to the reduction in the number of whorls. Additional study of the vascularization of flowers of *Sedum pusillum* (Sherwin & Wilbur, 1971), conducted to help clarify the generic lines between *Sedum* and *Diamorpha*, showed that *S. pusillum* does not fit into either Group III or Group IV. Sherwin & Wilbur suggest that the vascular pattern found in flowers of *S. pusillum*, which Quimby placed in Group III, is perhaps derived from the basic Group III pattern. Furthermore, their work indicates that more detailed investigations of individual species may show that floral vascularization in *Sedum* is more complex and variable than outlined by Quimby.

The carpels of *Sedum*, each of which is supplied by five vascular bundles, have been considered primitive since they are open during ontogeny, closing only during later development when the margins along the adaxial sutures are only slightly fused, and the marginal epidermal layers remain distinct (Eames, 1931). Henslow (1891) reported that the ventral carpel traces in *Sedum Telephium* are not inverted (a condition encountered in *Silene* and *Dianthus* [Caryophyllaceae] and in some species of *Rhododendron* subg. *Anthodendron* [Ericaceae]), but Subramanyam (1955) detected only inverted traces in species he examined. Relatively few investigations of the general vegetative anatomy of *Sedum* have been undertaken; see the works of Solereder (1899) and Metcalfe & Chalk (1950) for some details and references to most studies, as well as the more recent papers by Piaget (1966) and Jensen (1968).

Aspects of megasporogenesis and embryology of *Sedum* coincide with the general pattern given for the family with only a few significant exceptions. In *S. Telephium* subsp. *fabaria* (W. J. D. Koch) Kirschleger and *S. populifolia* Pallas (*Hylotelephium populifolium* (Pallas) H. Ohba), a subshrub from eastern Asia, an Allium-type megagametophyte has been reported to develop from the chalazal dyad cell, while in other investigated species a monosporic Polygonum-type is produced. Endosperm formation

is *ab initio* Cellular and a chalazal haustorium is developed, but Subramanyam (1963) found that in *S. ternatum* the haustorium remains 1-nucleate. *Sedum ternatum* is also distinguished by the presence of apical "caps" on the hooked synergids, structures that have been reported elsewhere only for *Helianthemum vulgare* (Cistaceae) and species of *Ribes* (Saxifragaceae or Grossulariaceae). See Subramanyam's articles (1955, 1963) for additional details and information about microsporogenesis.

Pollen of some European species of *Sedum* has recently been examined by 't Hart (1974), who found the grains to be 3- or rarely 2- or 4-zonocolporate. The sexine a, a tectum, is ornamented with short striae in a rugulate pattern, and, although considerable variation in morphology was evident, 't Hart concluded that the range of variation encountered within a single taxon, and occasionally within a single sample, equaled that found during the survey. All of the species examined (including one miscellaneous American species) belong to one variable pollen type and form a continuous morphological series that can only arbitrarily be divided into subtypes. However, 't Hart ventures to assert that within the *Rupestria* series species with low base chromosome numbers have relatively underived pollen subtypes, while those species with higher base numbers exhibit derived pollen subtypes. This correlation was not evident in the *Sedum acre* group, suggesting less phylogenetic unity within that taxon.

Determination of the generic relationships of *Sedum* is dependent, in large measure, on the delimitation of the genus and the several groups that have variously been either segregated from or included within the genus. At one extreme, as Moran (1942) points out, Kuntze (1898) concluded ". . . that all the species of the Crassulaceae with free carpels, i.e., practically the entire family, were best placed in the one genus *Sedum*." Conversely, there has been a continued tendency on the part of authors of floristic works (culminating in the treatments of Britton & Rose, 1903, 1905) to accord generic status to small groups or single species that within a local area appear distinct. In other instances, species or groups of species once included within *Sedum* have been removed and merged with other genera as warranted by careful analyses of relationships (e.g., *Hasseanthus* Rose, a segregate of *Sedum*, is now treated as a subgenus of *Dudleya* Britton & Rose, a member of subfam. Echeverioideae Berger).

In particular, sect. RHODIOLA is often recognized as a distinct genus, especially when the species of that section with which floristic workers are concerned have four-merous, imperfect flowers. *Sedum rhodanthum* of the Rocky Mountains (its flowers five-merous and perfect), like several of the Asiatic species, clearly belongs to the section as emended by Praeger, and it is transitional to species in other sections of the genus. However, despite the obvious similarities, *S. rhodanthum* was removed to the monotypic genus *Clementsia* by Rose (in Britton & Rose, 1903) in an attempt to create greater unity within sect. RHODIOLA, which Britton and Rose also treated as a genus. Similarly, species of sect. TELEPHIUM, some of which are transitional to sect. SEDUM, have been transferred to the segregate genus *Telephium* Hill, not L., or to *Anacampseros* P. Miller, and Ohba

has recently placed these species in the new genus *Hylotelephium*. In our area, in addition to recognizing *Diamorpha*, Britton and Rose also segregated *S. pusillum*, placing it in the monotypic genus *Tetrorum* Rose because of its annual duration and its four-merous flowers.

Certainly some of the problems of delimiting acceptable genera are due to the fact that affinities within the entire family appear to be interlinear as well as linear (Baldwin, 1939). Nonetheless, it is apparent that in the New World the closest affinities of *Sedum* are largely with genera of subfams. Sedoideae and Echeverioideae. Most of the closely allied genera of the Sedoideae share the characteristic terminal flowering stems and flowers with free, spreading petals, while genera of subfam. Echeverioideae are usually characterized by lateral flowering stems and by flowers with basally connate, erect or spreading petals. *Sedastrum* Rose (*Sedum* sect. *Sedastrum* (Rose) Berger) is distinguished from *Sedum* by its persistent, rosulate basal leaves and its flowers with enlarged nectaries and white petals, while *Parvisedum* R. T. Clausen (*Sedella* Britton & Rose, not Fourreau; *Sedum* sect. *Sedella* (Britton & Rose) Berger), a small genus of four annual species of the California mountains, is characterized by its carpels with solitary ovules. *Diamorpha* differs from *Sedum* in several significant respects discussed elsewhere, but the contrasts between *Villadia* Rose (including *Altamiranoa* Rose) are less concrete. Consisting of about 45 species of Mexico, Central America, and the Andes of South America, species of *Villadia* produce terminal inflorescences, and in the last analysis the genus is separated from *Sedum* only on the basis of the degree of basal connation of the petals (Moran, 1971). *Lenophyllum* Rose, a small genus of about five species restricted to the Gulf Coastal Plain of southern Texas and Mexico, is characterized by opposite leaves and flowers arranged in terminal racemose or spicate cymes. In habit the species of *Lenophyllum* resemble species of *Echeveria* DC. (ca. 143 species ranging from Texas to the Andes of South America), but Uhl & Moran (1953) suggest that *Lenophyllum*, which was once placed in subfam. Echeverioideae, is best removed to subfam. Sedoideae. Clausen (1975) contends that the genus was probably derived from the same phyletic line that gave rise to *Villadia*, *Echeveria*, and *Pachyphytum*.

While the relationships of the several genera of subfam. Echeverioideae are taxonomically complex and cytologically diverse and complicated (Uhl & Moran, 1953), it would appear that *Echeveria* is closely allied to *Sedum*. Walther (1936, 1972) speculates that *Echeveria* was derived from species not unlike certain subshrubby species of *Sedum* belonging to sects. PACHYSEDUM Berger and DENDROSEDUM Berger, which are endemic to Mexico (the center of diversity of *Echeveria*) and share the characteristic lateral flowering stems of subfam. Echeverioideae.[5] Although hybrids between species of *Echeveria* and *Sedum* sects. PACHYSEDUM and

[5] Walther employs the name *Sedum* sect. *Bergerosedum* Walther to refer to those species of the two sections mentioned above; some of these species were also treated by Rose as comprising the segregate genera *Cremnophila* and *Corynephyllum*. The sectional name, however, was nomenclaturally superfluous when published. In ad-

DENDROSEDUM have been produced (Walther, 1953; Uhl, 1966, 1967, 1970; one placed in the hybrid genus × *Sedeveria* Walther), this evidence of close relationship loses some of its potential significance due to the numerous intergeneric hybrids produced between *Sedum* and other genera of subfam. Echeverioideae (Uhl, 1966; Uhl & Moran, 1973; Knobloch, 1972).

Uhl & Moran (1973), considering the cytological evidence, indicate that many Mexican species of *Sedum* (where $x = 29–36$) belong to a comparium that includes, in addition to *Echeveria* (where $x = 27–34$), species of *Pachyphytum* Link, Klotzsch, & Otto, $x = 31–33$ (12 species of Mexico distinguished by pairs of scales on the adaxial surfaces of the petals), *Thompsonella* Britton & Rose (*Echeveria* sect. *Thompsonella* (Britton & Rose) Berger) (two species of south-central Mexico with the flowers arranged in a panicle or thyrse and with red lines on the adaxial surfaces of the petals), and *Graptopetalum* Rose (*Byrnesia* Rose; *Sedum* sect. *Graptopetalum* (Rose) Berger; *Echeveria* sect. *Graptopetalum* (Rose) Kearny & Peebles), $x = 30–35$ (11 species of Arizona and Mexico with red dots, often in transverse bands, on the adaxial surfaces of the petals). Uhl & Moran (1973, p. 655) state that the chromosomes of these taxa ". . . apparently have considerable homology for one another, as shown by their ability to pair, often more or less normally, in intergeneric hybrids. Very likely it was from an ancestral plexus with such [base chromosome] numbers, in the more primitive genus *Sedum*, that the other four genera were derived."

Plants of *Sedum Telephium* and other species are occasionally used as greens in salads, and Uphof (1968) reports that the Eskimos of Alaska eat the leaves of *S. Rosea* fresh, soured, or in oil. *Sedum acre* has apparently been used as a laxative, while the juice from plants of the Mexican and Guatemalan *S. dendroideum* Moç. & Sessé is astringent and has been used to harden gums and to treat chilblains and dysentery. The juice of this species has also been reported by Palarea (1954, as *S. praealtum* A. DC.) to cure opacities of the lens and cornea in humans. In addition, various medicinal uses have been reported for *S. Rosea*, and numerous studies of the chemical and physiological effects of this species have been conducted, primarily by Russian investigators; see Clausen (1975) for an extensive list of Russian references.

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2. Diamorpha Nuttall, Gen. N. Am. Pl. 1: 293. 1818.

Diminutive, characteristically red-pigmented winter annuals from slender primary roots and well-developed, fibrous secondary roots; plants developing ill-defined, over-wintering basal rosettes in fall, the erect or ascending, branched or unbranched stems developing in spring. Leaves alternate, sessile, cylindric-ovoid or cylindric-oblong, succulent, with entire margins and rounded apices (often appearing acute when dried). Flowers perfect, on short, distally thickened pedicels, arranged in leafy, compound cymose inflorescences or variously reduced to a simple dichasium or a single terminal flower. Sepals 4, very small, deltoid or deltoid-linear, persistent in fruit. Petals 4, alternate with the sepals, white or pinkish, strongly cucullate, the 4 opposite anthers held in small distal pockets until late in anthesis. Stamens 8, obdiplostemonous; filaments tapering gradually to the basifixed, reddish anthers. Gynoecium of 4 (rarely 5) carpels; carpels

united basally for ca. 1/3 their length, free above, each constricted into a short, beaklike style, the styles terminated by small capitate stigmas, apparently shriveling after pollination; ovary superior, 4- (rarely 5-) locular in the syncarpous region, each carpel 1-locular in the apocarpous region; ovules numerous on axile placentae below, pendulous on marginal placentae above. Carpels divergent, becoming obliquely oriented in fruit, producing a 4- (or 5-) beaked follicetum, each follicle dehiscing extrorsely by a tear-shaped, flaplike valve. Seeds several in each follicle, small, pyriform; seed coat reddish brown, finely granulate-striate; embryo large, with rounded cotyledons. Base chromosome number 9. TYPE SPECIES: *D. pusilla* sensu Nutt. non Michaux = *D. Smallii* Britton (cf. Wilbur, 1977). (Name from Greek, *di*, two, and *morphe*, form or shape, possibly in reference to the initial confusion of the type species with *Tillaea* or, more likely, *Sedum pusillum*; Baldwin (1940) interpreted the name as signifying "deformed or contrary formed.") — ELF-ORPINE.

An arresting monotypic genus endemic to the southeastern United States in North and South Carolina, Georgia, Alabama, and southeastern Tennessee. Growing in dense, usually pure populations in the shallow, humus-free soils of depression pits on exposed rock surfaces, *Diamorpha Smallii* Britton (*Tillaea ? cymosa* Nutt., *Diamorpha cymosa* (Nutt.) Britton ex Small, *D. pusilla* (Michaux) Nutt., *Sedum cymosum* (Nutt.) Fröd., *S. cymosum* var. *Smallii* (Britton) Fröd., *S. Smallii* (Britton) Ahles), $2n = 18$, is a conspicuous and consistent member of the vernal flora of granitic flat-rock communities of the upper and lower Piedmont of the Carolinas, Georgia, and eastern Alabama (McVaugh, 1943). Not totally restricted to granitic rock, *D. Smallii* also occurs in similar situations on sandstone outcrops and on sandy flats in Georgia, on the Cumberland Plateau of southeastern Tennessee, and in the mountainous regions of northeastern and central Alabama.

When *Diamorpha Smallii* was first discovered, apparently at Flat Rock, north of Camden, South Carolina, the type locality of *Sedum pusillum* Michaux, Nuttall confused plants of the two taxa, and, although the initial confusion was later clarified by Asa Gray (1876), the nomenclature of *Diamorpha* has been troublesome and further complicated by controversy over the acceptance of *Diamorpha* as a genus distinct from *Sedum*. Aspects of nomenclature have been clarified only recently by Wilbur (1964, 1977), who has applied the correct specific epithet, *Smallii*, to the single species. The name *Diamorpha Smallii* was originally proposed by Britton for a reputed second species (treated as a variety by Fröderström, 1935) based on immature plants that do not differ from other plants of *Diamorpha* of an equal developmental stage. See Wilbur's papers for the rationale behind the adoption of Britton's epithet, as well as for historical and other nomenclatural details.

The controversy over the distinctness of *Diamorpha* as a genus has undoubtedly stemmed from the overall morphological resemblance of *D. Smallii* and *Sedum pusillum*, as well as from their almost identical distri-

bution and close ecological association. Moreover, McCormick (in McCormick & Platt, 1964) reported natural and artificial hybrids between *Diamorpha* and *Sedum* (presumably *S. pusillum*), but such hybrids have not been documented (cf. Sherwin & Wilbur, 1971).

Diamorpha has several distinctive morphological features, anatomical differences, and a chromosome number uncommon in *Sedum*, all of which substantiate generic status. *Diamorpha* is unique in the dehiscence of its follicles by flaplike abaxial valves (FIGURE 2, e), a type not found elsewhere in the Crassulaceae. The absence, except during developmental stages, of an adaxial suture line on the carpels and the coherence of the carpels at the base for about one-third their length further separate *Diamorpha* from *Sedum* in general, while its cucullate petals, its floral vascularization pattern (Sherwin & Wilbur, 1971), its usually deeper red pigmentation, and its different ecological niche separate *D. Smallii* from *S. pusillum* in particular.

As a winter annual rarely more than 10 cm. tall, *Diamorpha Smallii* has attracted the attention of several investigators (McCranie, McVaugh, Wiggs & Platt, McCormick & Platt, McCormick *et al.*, Sharitz, Baskin & Baskin, and Sharitz & McCormick) who have studied its life cycle and aspects of its ecology under both field and laboratory conditions to determine its specific adaptations to its unique habitat. As a result, *Diamorpha* is one of the biologically better-known taxa in the southeastern flora.

Seeds of *Diamorpha* germinate during late October and early November, a period of autumn rains and warm daytime temperatures (ca. 20° C.).

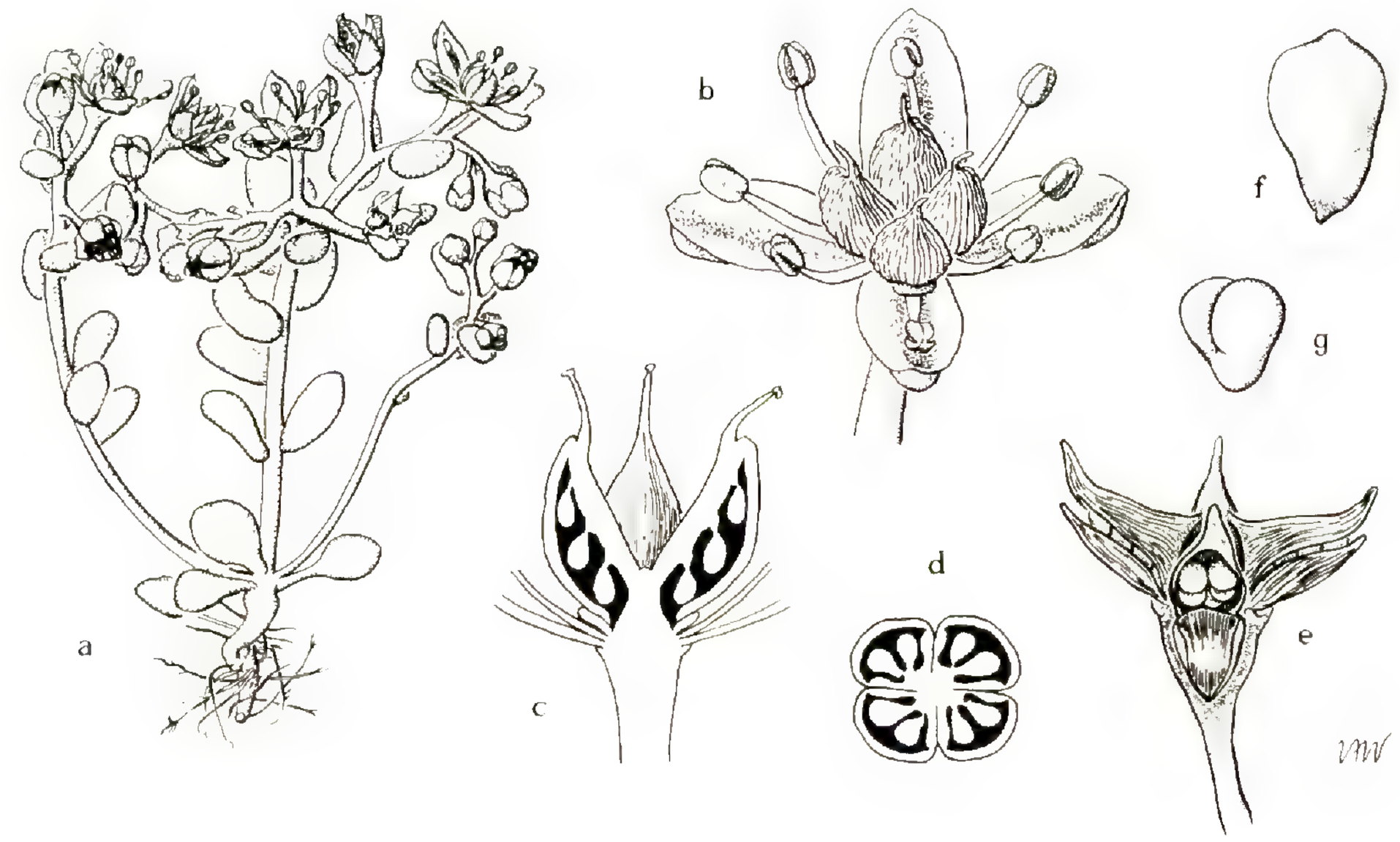

FIGURE 2. **Diamorpha**. a–g, *D. Smallii*: a, habit of flowering plant, × 1½; b, flower, × 8; c, longitudinal section through immature follicles (note nectaries at base of staminal filaments) showing pendulous ovules, × 10; d, cross section through four carpels of gynoecium in basal, syncarpous region, × 10; e, dehisced follicles, × 6; f, seed, × 30; g, embryo, × 25.

Although germination occurs readily under these conditions, seedling establishment is dependent on extensive secondary root development that, in turn, requires a substrate pH in the narrow range of 4.5 to 5. During establishment, plants can tolerate three or four weeks of total inundation or two to three weeks of desiccation before dying. If established, the plants assume a compact, rosette-like form, develop their characteristic deep red pigmentation, and become semidormant, with little further vegetative growth. Resistant to frost, the plants resume growth and initiate flower-bud primordia during late February. Branching and height of plants are determined at this time and are correlated with soil factors and competition, the latter of which is in turn related to population density. The inflorescences expand during March, and, depending upon locality, anthesis begins during late March and early April, reaching its peak toward the middle of April.

Details of the pollination ecology and breeding system have not been studied in great detail, but it has been noted that the four anthers opposite the sepals dehisce at the onset of anthesis, while the remaining four, which are held by the four petals, have a retarded dehiscence, shedding pollen toward the end of flowering. Bees and other unidentified insects have been observed visiting the flowers, and cross-pollination is to be expected.

Death of plants within a population begins by the middle of April, and by the middle of May most of them are dead. According to Wilbur, seed release from the mature follicles occurs by late spring and early summer, an observation contrary to Wiggs & Platt's finding that follicle dehiscence does not occur until late summer or fall, "until the continued action of moisture . . ." causes dehiscence, "a process requiring 2–5 months." According to Wiggs & Platt, retention of the seeds in the follicles above the outcrop surface over summer, during which time the seeds after-ripen, is an adaptive mechanism that protects the seeds from exposure to the high summer temperatures of the outcrop surfaces.

Observations of a series of populations of *Diamorpha* both in the field and in transplant studies on a simulated outcrop led McCormick & Platt to conclude that "*Diamorpha* is undergoing ecotypic variation," inasmuch as clinal phenological variation on a northeast to southwest gradient was detected and physiological differences between populations, related primarily to moisture gradients, were found. They summarized their findings and those of other investigators, saying that *Diamorpha* "has become adapted to the rigorous outcrop environment, both through drought evasion and drought tolerance. All stages of the life-cycle express unusual tolerances to extremely low or high moisture levels, and the entire life-cycle is adapted to make maximum use of favorable intensities and durations of moisture and to avoid periods of low moisture and high temperature."

The relationships of *Diamorpha* would appear at first glance to be with annual species of *Sedum*, yet certain evidence does not support this hypothesis. Fröderström (1935) allied *Diamorpha* (as *Sedum cymosum*) with *S. pusillum*, $2n = 8$, and *S. Nuttallianum* Raf., $2n = 10$, in his group 8, EPETEIUM AMERICANUM, and suggested affinities of this group with annual

European and Asiatic species. Baldwin (1940), like Berger (1930), maintained the generic status of *Diamorpha* and proposed that the genus might represent "amphidiploid results of fusion between representatives of the 4- and 5-chromosome tendencies" found within annual species of *Sedum*. However, Baldwin also suggested the possibilities of affinities with *Tillaea* of subfam. Crassuloideae.

The anatomical studies of floral vascularization conducted by Sherwin & Wilbur (1971) have shown, however, that Fröderström's group 8 is "highly heterogeneous." The differences between the taxa were seen by Britton & Rose to be sufficient to place the three species in different genera, viz., *Diamorpha, Tetrorum* (to include *Sedum pusillum*), and *Sedum*. The rather enigmatic and apparently isolated position of *Diamorpha* within the Crassulaceae was recognized by De Candolle (1828), who established the tribe Crassulaceae Anomalae to include *Diamorpha* and *Penthorum* L.

Torrey & Gray (1840) also grouped these two genera together in the crassulaceous tribe Diamorphae, a tribe maintained by Small (1933) for *Diamorpha* alone. It is probable that *Diamorpha* and the taxa to which it has been allied share superficial resemblances as a result of similar selection pressures and represent convergent groups within the Crassulaceae. In a family notorious for indistinct generic limits, the distinctiveness of *Diamorpha* is probably indicative of relatively great age.

Although no local uses have been recorded for *Diamorpha*, the plant has been important as a subject of continued biologic investigation. With the current knowledge of its life cycle, *Diamorpha Smallii* will undoubtedly continue to be valuable as an easily manipulated experimental plant.

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Subfam. CRASSULOIDEAE

3. **Crassula** Linnaeus, Sp. Pl. 1: 282. 1753; Gen. Pl. ed. 5. 136. 1754.

A diverse, polymorphic genus of diminutive [to large], prostrate to erect, aquatic or semi-aquatic [to xeromorphic], herbaceous [to subshrubby], branched [or unbranched], mostly succulent annuals, biennials [or monocarpic or polycarpic perennials], usually from fibrous roots [or occasionally from tuberous rhizomes], the plants of mosslike aspect, often rooting at the nodes. Leaves opposite, small and inconspicuous [or usually of moderate size, or rarely lacking and the internodes swollen], sessile [to distinctly petiolate], the internodes elongate [or often reduced in length and the leaves clustered and subrosulate, variously imbricate, or decussate and 4-ranked, the arrangement and shape of the leaves often giving the plants a *Lycopodium*-like or bizarrely geometric appearance], the leaf bases often connate and sheathing, the blades usually glabrous [or variously pubescent, sometimes with structural "windows" and sub-

cuticular air bladders], with entire [or crenate or serrulate] margins. Flowers usually small, 3-, 4-, [or 5-, rarely 6–9-] merous, solitary [or sometimes clustered] in the axils of leaves [or terminal, usually arranged in terminal or axillary corymbose, thyrsoid, or subumbellate inflorescences, occasionally with bulbils or plantlets replacing the flowers]. Sepals small, greenish, shorter than the petals, ± erect [or flared], often connate at base. Petals small, [erect to] spreading, of various shapes, white [to pinkish or sometimes yellowish], greenish [or bluish], usually connate at base, [often with a small subapical mucro]. Stamens the same number as the petals, insertion hypogynous [or epipetalous on the shallow corolla tube], opposite the sepals, the filaments subulate to flattened or filiform, with ovate to oblong, basifixed anthers [sometimes with conspicuous connectives]. Gynoecium of 3–5 or rarely more, erect [or divergent], free or basally connate carpels, the carpels tapering [gradually] or abruptly to short and thick [or long and slender] styles, the stigmas small, terminal [or sometimes subapical]; ovaries unilocular, with 1, 2, or several to many ovules on placentae along the adaxial sutures. Fruits erect [or divergent] follicles, often with short stylar beaks, dehiscent along the adaxial sutures; seeds 1 to many, small, the embryo surrounded by endosperm. Base chromosome numbers 7, 8. (Including *Bulliarda* DC., *Hydrophila* House, *Tillaea* L., *Tillaeastrum* Britton.) LECTOTYPE SPECIES: *C. perfoliata* L.; see Hitchcock, Prop. Brit. Bot. 143. 1929. (Name from Latin, *crassus*, thickish, in reference to the thick, succulent leaves and stems of many of the species.) — CRASSULA.

A large, polymorphic, and ecologically diverse genus of nearly 300 species restricted in distribution, with the exception of members of one of the seven sections, to southern Arabia and to sub-Saharan Africa. The genus has its center of diversity, both in number of species and in morphological variation, in southern Africa. Unlike the species of sections restricted to Africa, members of sect. TILLAEOIDEAE DC. emend. Schönl., to which the following discussion is largely limited, are cosmopolitan in distribution, occurring on all continents except Antarctica. They are, moreover, the only representatives of the Crassulaceae in southern South America, New Zealand, and Australia.

In the southeastern United States sect. TILLAEOIDEAE is represented by *Crassula aquatica* (L.) Schönl. (*Tillaea aquatica* L., *T. simplex* Nutt., *Tillaeastrum aquaticum* (L.) Britton, *Hydrophila aquatica* House, *Bulliarda aquatica* (L.) DC., *Elatine tetrandra* Maxim.; including *Crassula Drummondii* (Torrey & Gray) Fedde), water pigmy, $2n = 42$, which has a documented distribution only in Louisiana. It may also occur in North Carolina,[6] and Hultén (1958) maps a locality for the species in the panhandle of Florida. Elsewhere in North America it occurs along the eastern

[6] One specimen of *Crassula aquatica* in the Gray Herbarium has been considered an M. A. Curtis collection from North Carolina, but the collection data do not appear to date from Curtis's time. Radford, Ahles, & Bell (1968) do not report the species for the Carolinas.

seaboard from Quebec and the Canadian Maritime Provinces, southward into New England, New York, Delaware, and Maryland, and along the Pacific coast in Alaska, Washington, Oregon, and California. Fassett (1928, p. 106) suggests that in northeastern North America *C. aquatica* is probably a preglacial relic ". . . which has found estuarine conditions favorable for its existence." Inland, it has been collected from scattered, disjunct localities in the Canadian Northwest Territories (Mackenzie District), and in Minnesota, Nevada, Utah, Colorado, Wyoming, and New Mexico. Beyond North America *C. aquatica* has a wide, disjunct distribution in Asia and northern Europe.

A minute, glabrous annual or biennial with prostrate and nodally rooting to ascending or erect, usually branched stems, *Crassula aquatica* is tolerant of both fresh and brackish water. In the Northeast, it is most often found growing in estuarine situations or in the mud or wet sand of receding pond margins where it often forms mosslike mounds. In northern Louisiana, where the species has been found to be relatively common (Thomas, 1971), it is usually found growing in the moist depressions of animal or vehicle tracks in pastures and old fields. Due to its insignificant stature, it is probably often overlooked by collectors, and Thomas has classified the species as a "belly-plant." The small, usually four-merous, greenish or white flowers are solitary in the axils of the connate-sheathing leaf blades and are borne on short pedicels that usually elongate in fruit.

The variable pedicel length of flowering plants of *Crassula aquatica* and the tendency for the pedicels to elongate after anthesis have led both to confusion between species and to the recognition of a segregate species. Plants from Louisiana to Mexico and from California and Washington with the pedicels longer than the subtending leaves in fruiting specimens have been segregated as *C. Drummondii* (Torrey & Gray) Fedde (*Tillaea Drummondii* Torrey & Gray, *Tillaeastrum Drummondii* (Torrey & Gray) Britton, *Tillaea aquatica* var. *Drummondii* (Torrey & Gray) Jepson), but such segregation is artificial when the range of pedical length within *C. aquatica* is considered, and most authors now include *C. Drummondii* within *C. aquatica*. Other plants from Prince Edward Island with the flowers distinctly pedicellate were originally confused with *C. Vaillantii* (Willd.) Roth, a species of Central Europe and northern Africa.

While there has been confusion about the other species of *Crassula* sect. TILLAEOIDEAE that occur in North America, it appears that only two additional ones have been found in the United States. Britton & Rose (1905) included two others as occurring in Mexico. *Crassula erecta* (Hooker & Arnott) Berger (*Tillaea erecta* Hooker & Arnott, *C. minima* Miers), sand pigmy, $2n$ = ca. 16, ca. 20–25, a species of dry, open locations, is native from southern Oregon southward, through California and Arizona, into Baja California; it also occurs disjunctly in Chile. *Crassula muscosa* (L.) Roth (*Tillaea muscosa* L.), a European species, has been reported from Amador and Calaveras counties, California. It has apparently become naturalized in the Great Valley of California and in an area in the southern North Coast Ranges (Clausen, 1975, p. 608).

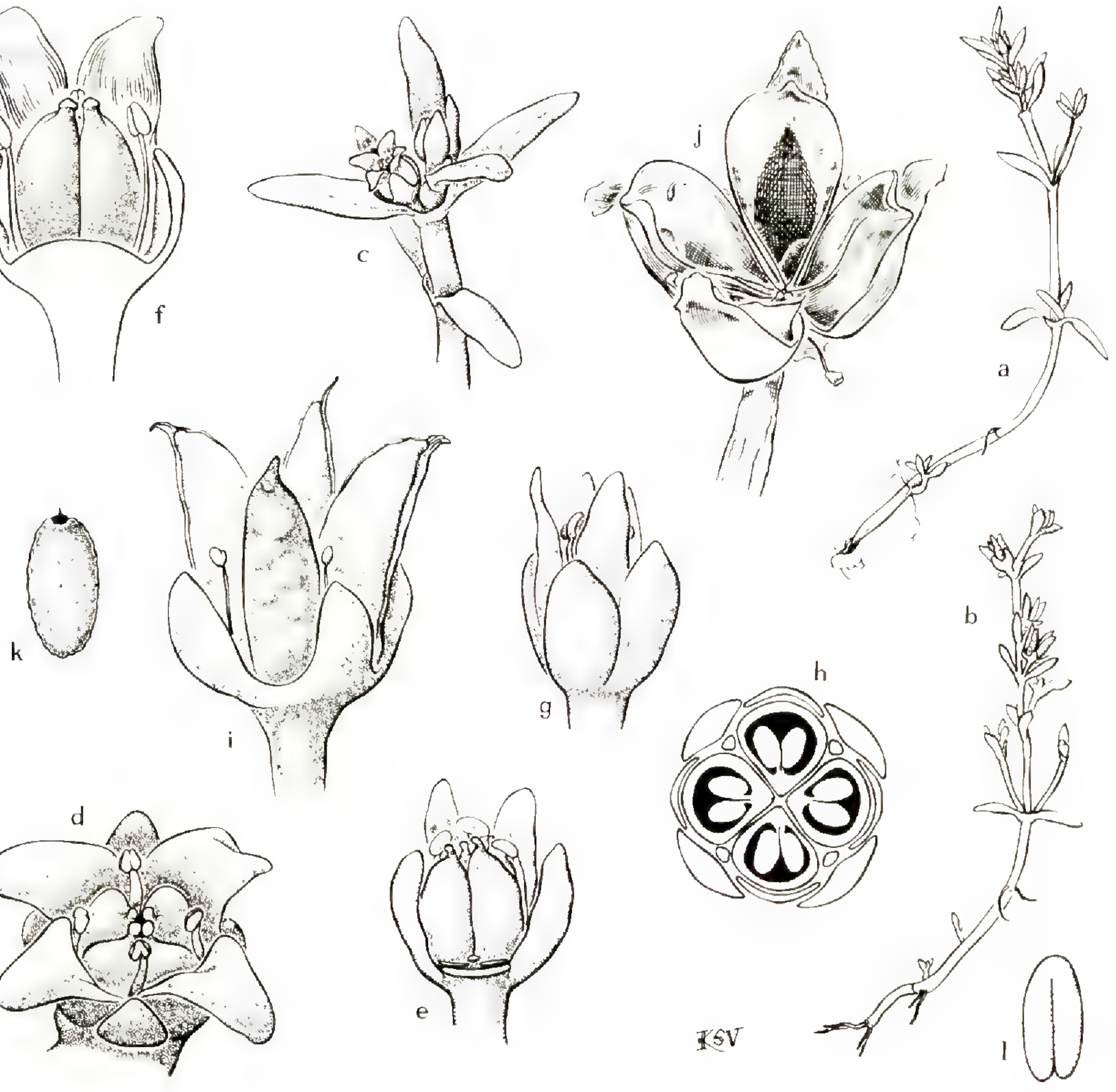

FIGURE 3. **Crassula**. a–l, *C. aquatica*: a, b, two plants, × 3; c, tip of shoot with axillary flower, × 6; d, flower, × 25; e, flower with petals and one stamen removed (note nectaries at base of carpels), × 25; f, longitudinal section through flower, two carpels removed, × 25; g, flower after anthesis, × 25; h, cross section through flower after anthesis, × 25; i, immature follicles, × 25; j, dehisced follicles, × 20; k, seed, × 50; l, embryo, × 50.

The union of *Tillaea* L. with *Crassula* has not been universally accepted. Authors of many floristic works have retained *Tillaea*, and some have divided *Tillaea* itself into small genera. Britton (1903), for example, established *Tillaeastrum* for species (*C. aquatica*) with solitary flowers and several-ovuled carpels, retaining *Tillaea*, sensu stricto, for species with clustered flowers and with carpels containing one or two ovules (e.g., *C. erecta*). However, as defined by Schönland, sect. TILLAEOIDEAE, comprising several groups or series,[7] combines these and other species that had otherwise been treated as segregate genera or sections of *Crassula*. Segregate taxa have been based primarily on the number of floral parts, ovule number, and nectar-scale shape. But, as Schönland (1916, p. 42) notes, these characters are "useless for generic distinction, as they may

[7] Schönland gave no rank to his subdivisions of sect. TILLAEOIDEAE; Jacobsen (1970) has designated them as series.

separate species which are otherwise closely allied and moreover they are sometimes not constant in one and the same species."

As a group, species of sect. TILLAEOIDEAE consist of small, morphologically variable, annual, biennial, or perennial plants adapted to wet soils (some are true aquatics), while others are decided xerophytes. The petals, which are usually spreading at anthesis, never form an urceolate corolla (a condition Schönland considers to be a xerophytic adaptation), and they lack the subapical mucro characteristic of *Crassula* sensu stricto. Despite these deviations, Schönland states that "no sharp line can be drawn between the Tillaeoideae and other sections of *Crassula*." He suggested further that species of sect. TILLAEOIDEAE are the least derived species of *Crassula* and that a great age for the section could be deduced from the widespread distribution of its species. Fröderström (1930, 1931) went so far as to suggest that *Tillaea*, which he maintained as a genus, was ancestral to the entire Crassulaceae. But Berger (1930) cautioned that species of the TILLAEOIDEAE are probably highly derived, reduced forms, an opinion shared by Uhl (1948), who suggested that the wide distribution of the section (and of individual species) is attributable to very efficient seed dispersal. Quimby (1971), who studied the floral anatomy of *C. aquatica*, also suggests that *Tillaea*, as a genus, could be considered a reduced form of *Crassula*.

Among other genera of the Crassulaceae, Schönland favored a possible origin of *Crassula* from the usually obdiplostemonous genus *Sedum*. Some species of *Sedum* sect. EMPETEIUM Boiss. (*Sedum* sect. *Procrassula* (Griseb.) Schönl., pro parte, *Procrassula* Griseb.) are haplostemonous, and, except for their alternate leaves, are suggestive of *Crassula*. The idea of an origin of *Crassula* from *Sedum* is given some support by Mauritzon (1933), who, on the basis of embryological data, concluded that *Crassula* (and *Tillaea*) is evolutionarily younger than *Sedum*. Quimby (1971) states that floral anatomical evidence, i.e., the single whorl of stamens and the lack of or small size of certain carpel traces, also supports this hypothesis.

Interspecific hybrids in *Crassula* appear to be very rare. However, the presence of an extensive polyploid series suggests reticulate relationships among the species. That sect. TILLAEOIDEAE has a base chromosome number of $x = 8$, as was suggested by Baldwin (1936), has been confirmed by the recent investigations of Merxmüller *et al.* (1971) and Friedrich (1973); yet the one discordant count for the section is that of $2n = 42$ for *C. aquatica*. Otherwise, somatic numbers range from 16 to ca. 128, all multiples of eight. Most other sections of *Crassula* have a base chromosome number of 7 (from the diploid to the decaploid level), but some sections share both base numbers. As noted by Uhl (1956), "the significance of the different basic chromosome numbers with respect to taxonomy is not yet known," but Friedrich asserts that "polymorphic aggregates, e.g. the *Crassula lycopodioides* complex, are extremely heterogeneous with regard to their caryological conditions. It appears that different species have been united often unjustifiedly in such cases."

The ease by which plants of *Crassula* species are propagated vegetatively has enhanced the use of these succulents as house plants. *Crassula lycopodioides* Lam., $2n = 16, 32, 48, 64, 96$ (sect. TILLAEOIDEAE series *Lycopodioides* Schönl.) and *C. pyramidalis* Thunberg, $2n = 14, 28$ (sect. PYRAMIDELLA Harvey), both of South Africa, are but two of the many species of *Crassula* available at florist shops. Perhaps the best known species is *C. argentea* Thunberg (*C. portulacea* Lam.), $2n = 42, 56$ (sect. STELLATAE Schönl.), also of South Africa and commonly known as the jade tree or Chinese rubber tree. Widely grown as a house plant, it is sometimes grown out-of-doors in warmer temperate regions as a perennial ornamental. The nomenclature and taxonomy of these and other species, however, is often confused and open to dispute, a situation due in large measure to the difficulties of preparing adequate, identifiable herbarium specimens of succulent plants.

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Subfam. KALANCHOIDEAE Berger

4. **Kalanchoë** Adanson, Fam. Pl. 2: 248. 1763.

Glabrous or pubescent, [monocarpic or] polycarpic perennial herbs, subshrubs, or shrubs, often of twining or rambling habit, the majority terrestrial from fibrous roots [or some epiphytic], many gemmiparous and viviparous. Leaves opposite and decussate or in whorls of 3, simple or occasionally pinnately compound, the simple leaves sessile to petiolate, the bases of the blades or the petioles often amplexicaul; blades ± succulent, flattened to ± cylindrical with entire, crenate, dentate, or pinnatisect margins, often with adventitious buds in the crenations of the leaf margins producing plantlets. Flowers perfect, usually numerous, erect to pendent in terminal or sometimes axillary, bracteate, paniculate or cymose inflorescences, sometimes with adventitious buds in the axils of the bracts; insertion of the calyx and corolla hypogynous. Sepals 4, weakly to strongly connate, forming a cylindrical, often inflated calyx tube, the 4 free lobes shorter to longer than the tube. Petals 4, violet through red and pink to white, yellow, or greenish, connate for most of their length, forming a cylindrical to ± campanulate or ± urceolate, usually 4-angled corolla tube, the tube sometimes basally constricted over the gynoecium and the 4 free lobes spreading to recurved. Stamens 8 [or rarely 4], epipetalous in 2 whorls of 4, usually exserted; filaments slender, tapering to the basifixed, yellowish anthers. Gynoecium 4-carpellate, the erect or divergent carpels connate at least basally; carpels constricted above the ovaries into slender, usually included styles, the stigmas small,

often poorly or not differentiated; ovaries unilocular with numerous anatropous ovules on placentae along the adaxial sutures. Fruits erect or divergent, papery to coriaceous follicles dehiscent along the adaxial sutures; seeds numerous, very small, usually ± oblong and with rugose or wrinkled seed coats; embryo straight, small, embedded in endosperm, the megagametophyte of the Polygonum type. Base chromosome numbers 17, 18, 20. (*Vereia* Andrews, including *Bryophyllum* Salisbury, *Kitchingia* Baker.) TYPE SPECIES: *K. laciniata* (L.) A. P. de Candolle. (Name apparently derived from the Chinese name for one of the species; cf. W. H. Harvey in Harvey & Sonder, Fl. Capensis 2: 327–380. 1894.) — KALANCHOË, BRYOPHYLLUM.

Approximately 125 species in three sections, the large majority endemic to Madagascar, others indigenous to Africa and Socotra, one or two widely distributed in both the Old and New World tropics. In the southeastern United States eight species have been reported as naturalized, all in southern Florida. Lakela & Craighead (1965) included three species in their checklist, while Long & Lakela (1971) considered six. Recent collections by Brumbach on Captiva and Sanibel islands, Lee County, indicate that one or two additional species have become established, primarily on the latter island.

Six of the eight species occurring in our area belong to sect. BRYOPHYLLUM (Salisb.) Boiteau & Mannoni (*Bryophyllum* Salisb.), a section characterized by opposite or usually whorled leaves, pendent flowers with tubular, often inflated calyces with the lobes shorter to longer than the tube, the corollas often constricted basally with the stamens inserted near the base, and the carpels erect. Plants of many species of this section produce plantlets in the crenations of the leaves. The remaining four naturalized species are members of sect. KALANCHOË and are characterized by opposite leaves, erect flowers with the calyx of free or basally united sepals, unconstricted corollas with the stamens inserted at or near the middle, and erect and contiguous carpels. In species of sect. KALANCHOË, plantlet production is apparently restricted to cut or injured surfaces. The third section, KITCHINGIA (Baker) Baillon (*Kitchingia* Baker), composed of plants with opposite leaves, pendent to nodding flowers with the calyx lobes about as long as the calyx tube, basally constricted corollas with the stamens inserted near or above the middle, and divergent carpels, is not known to be represented in the southeastern United States.

Of the species belonging to sect. BRYOPHYLLUM, *Kalanchoë pinnata* (Lam.) Persoon (*Cotyledon pinnata* Lam., *Bryophyllum calycinum* Salisb., *B. pinnatum* (Lam.) Kurz, *Sedum madagascaricum* Clus.), $2n = 36$, 38(?), 40, is undoubtedly the most widely naturalized species in our area. Often forming dense colonies in waste and disturbed areas, it has been reported from Palm Beach, Hendry, Lee, Collier, Monroe, and Dade counties. Plants of *K. pinnata*, which can reach two meters in height, are easily recognized by their hollow stems and their large paniculate inflorescences of flowers with papery, inflated, greenish white to pinkish or

reddish calyx tubes 2.5–4 cm. long. Initially producing simple leaves with crenate margins, mature plants develop pinnately compound leaves with three or five leaflets. Both types of leaf produce plantlets in the crenations of the margins, and it is by this vegetative means that extensive colonies of plants have developed. Widely distributed throughout the tropics and subtropics of both hemispheres, it is probable that much of the wide range of *K. pinnata*, the nativity of which is uncertain, is due to the activities of man.

Flowers of *Kalanchoë Gastonis-Bonnieri* Hamet & Perrier, $2n = 34$, are similar to those of *K. pinnata* but are smaller, and the calyces are less inflated. The corollas, which extend beyond the calyx tubes, are either yellowish green or reddish, but apparently only the latter color form is represented in our flora. The plants produce large, consistently simple, lanceolate to spatulate, whitish to purplish leaves, sinuate to crenate at the margins. Native to Madagascar, *K. Gastonis-Bonnieri* has become well established on Sanibel Island, Lee County, Florida.

Kalanchoë tubiflora (Harvey) R. Hamet (*Bryophyllum tubiflorum* Harvey, *K. delagoënse* Eckl. & Zeyh., *B. delagoënse* (Eckl. & Zeyh.) H. Schinz; including *K. verticillata* Scott-Elliot, *B. verticillatum* (Scott-Elliot) Berger), $2n = 34, 40, 68$, has also been reported as naturalized in several areas of Florida in Martin, Palm Beach, Lee, and Collier counties, where it has been noted growing in waste places and on shell mounds. Widely grown as a pot plant, *K. tubiflora* is characterized by its distinctive violet-brown-spotted, more-or-less cylindrical leaves that are shallowly grooved on the adaxial surface and notched at the apex where bulbiferous spurs produce an abundance of plantlets. The flowers, which are notable for their relatively short calyces but long, pinkish to red corollas with spreading lobes, are produced in cymose corymbose inflorescences. Native to Madagascar, *K. tubiflora* is probably indigenous to areas of South Africa as well.

Also well known as a pot plant, *Kalanchoë Daigremontiana* Hamet & Perrier (*Bryophyllum Daigremontianum* (Hamet & Perrier) Berger), $2n = 34$, has become established in Palm Beach County and on Sanibel Island, Lee County. It has also been collected at Key West and may be naturalized elsewhere in the Florida Keys. The erect, glabrous, robust plants of this species, which is native to Madagascar, attain one meter in height and produce decussate, petiolate leaves with large, succulent blades that are spotted or blotched reddish brown beneath and are often ± auriculate at base. Abundant plantlets are produced by adventitious buds in the notches along the crenate to serrate margins. The pendent, lavender flowers are similar to those of *K. tubiflora*.

Kalanchoë laxiflora Baker (*Kitchingia laxiflora* Baker, *Bryophyllum crenatum* Baker, *Kalanchoë Tieghemi* Hamet, *K. crenata* Hamet, not Haw.), $2n = 34$, also native to Madagascar, has been reported as naturalized in waste places in Collier, Monroe, and Dade counties. A glabrous perennial to 5 dm., *K. laxiflora* is easily distinguished by its decussate, petiolate leaves with variable ovate to pandurate blades with crenate margins and ± auriculate bases. Like the other species of sect. Bryo-

PHYLLUM, plants of *K. laxiflora* produce plantlets in the crenations of the leaves. The flowers, with short, ± inflated calyces and relatively long, red to rosy- or yellowish-orange corollas, are produced in branched, paniculate inflorescences.

Unlike other naturalized species of sect. BRYOPHYLLUM, plants of *Kalanchoë Fedtschenkoi* Hamet & Perrier, $2n = 34$, develop into low, dense, many-branched shrubs with procumbent stems that eventually turn upward. Long, stiff adventitious roots are produced along the procumbent parts of the stems, and the short-petiolate, decussate leaves are closely spaced. The bluish green blades are ovate with rounded apices, and the crenate margins are brownish tinged in the crenations. The flowers, produced in terminal dichasial inflorescences, are brownish pink. Another native of Madagascar, *K. Fedtschenkoi* is known to be established in our area only on Sanibel Island, Lee County, Florida.

Of the two species of sect. KALANCHOË that are naturalized in our area, *K. marmorata* Baker (*K. grandiflora* A. Rich., not Wight & Arn., *K. somaliensis* Baker, *K. macrantha* Baker), $2n = 34$, is perhaps the most distinctive. A glabrous shrub usually branched from the base and with erect or sometimes procumbent stems, plants of *K. marmorata* are easily recognized by their sessile to shortly petiolate leaves with undulating to crenate margins that are green to plum colored and often brownish spotted on both surfaces. The erect flowers, borne in corymbose cymes, are characterized by long, white corolla tubes, 8–10 cm. long, terminated by short, deltoid lobes. Native to Ethiopia and Somalia, it is reported by Long & Lakela (1971) to be established in hammocks and disturbed sites in southern Florida, where it often forms extensive colonies.

Kalanchoë crenata (Andr.) Haw. (*Veria crenata* Andr., *K. integra* (Medic.) O. Kuntze var. *crenata* (Andr.) Cufodontis), a shrub with long-petiolate, elongate-lanceolate leaves with doubly dentate margins and yellow flowers produced in glandular-pubescent inflorescences, is the second species of sect. KALANCHOË naturalized in Florida. Long & Lakela (1971) list it as occurring in disturbed sites and hammocks in South Florida, and I have seen a specimen collected in 1973 from Sanibel Island, Lee County. Considerable taxonomic and nomenclatural confusion apparently surround *K. crenata*, and plants of this and closely allied taxa have been given varying taxonomic recognition (cf. Bailey *et al.*, 1976; Jacobsen, 1960, 1970; Baldwin, 1938; and Long & Lakela, 1971). As a result, various names, including *K. laciniata* (L.) DC., have been applied to our plant, apparently a South African native, and taxonomic and nomenclatural aspects need clarification. Baldwin (1938) found $2n = 34$ and $2n = 68$ for plants of this complex supposedly corresponding to *K. laciniata*, sensu lato, and $2n = 102$ for plants determined as *K. crenata*.

Much of the taxonomic attention given *Kalanchoë* has centered around its generic boundaries and the validity and status of *Bryophyllum* and *Kitchingia*. Many botanists have followed Baillon (1885), who included *Kitchingia* as a section of *Kalanchoë*, and Hamet (1907, 1908), who in-

corporated both *Bryophyllum* and *Kitchingia* within *Kalanchoë* as the sole genus of subfam. Kalanchoideae. Hamet placed the species in 14 groups of undesignated rank, while Boiteau & Mannoni (1947–1949) arranged the species in three sections (and numerous subsections) that reflect the originally proposed generic boundaries.

Those who have maintained or supported the maintenance of three genera have included Berger (1930), and Tillson (1940), who offered anatomical evidence in support of her position. Tillson found that in all three taxa ". . . the four petal traces are adnate to the corresponding antepetalous stamen trace as it leaves the floral axis." Despite the level of stamen insertion, however, consistent differences in the level of divergence of the two traces were noted. In *Bryophyllum* the traces separate below the level of corolla insertion, while in both *Kalanchoë*, sensu stricto, and *Kitchingia* separation occurs at some level in the corolla.

However, the intermediate morphology of several species originally indicated that the three genera should be treated as one, and this position has been supported by interpretations given both embryological (Mauritzon, 1933) and cytological (Baldwin, 1938) data. More recently, Friedmann (1971), who has surveyed the chromosome numbers of numerous Madagascan kalanchoës, has cautioned that additional cytological data together with geographical evidence may indicate that two genera, *Bryophyllum* (including *Kitchingia*) and *Kalanchoë*, are justified. It is obvious that additional evidence will be required to validate either the continued use of one genus or of two or three genera, and to gain unanimity among botanists. The choice made here to consider subfam. Kalanchoideae as consisting only of *Kalanchoë*, itself comprising three sections, is provisional — a choice of convenience that preserves the identity of the three taxa, yet reflects what are very close and undoubtedly reticulate relationships between them.

Chromosomes of *Kalanchoë* are small, yet chromosomal morphology is generally discernible and may be variable within a species complement; heterochromatic fragments have also been observed in several species. Chromosome numbers have been reported to range between $2n = 34$ and $2n =$ ca. 500, but most species are either diploid with $2n = 34$ or 36, or tetraploid with $2n = 68$ or 72. *Kalanchoë crenata* is probably a hexaploid with $2n = 102$; *K. Grandidieri* Baillon, $2n =$ ca. 140, is likely an octoploid; and *K. Faustii* Font Quer is a decaploid with $2n = 170$. Multivalent or secondary associations during meiosis apparently are uncommon.

While the majority of species of sect. KALANCHOË have chromosome numbers based on 18, and most of those of sects. BRYOPHYLLUM and KITCHINGIA are based on 17, there is incomplete coincidence between base chromosome number and sectional lines. Baldwin (1938) proposed that, of the possible base numbers for the genus, viz. 17, 18, 20, the primary number is 17. His suggestion was based on the hypothesis that *Kalanchoë* had an origin involving members of subfams. Crassuloideae and Cotyledonoideae Berger where base chromosome numbers of 7 or 8 and 9,

respectively, were suspected. Both subfamilies are well represented in the geographical area where *Kalanchoë* is indigenous.

Although the prevalent diploid number found in *Kalanchoë* is 34, a number based on 17, Uhl (1948) proposed that the Kalanchoideae may have had an origin completely within the Cotyledonoideae, and that, as a result, the primary base chromosome number for *Kalanchoë* is 18. Uhl's proposal is strengthened if members of *Crassula* sect. TILLAEOIDEAE are considered to be derived members of that genus. This interpretation requires that, of the two possible base numbers for the Crassuloideae, 7 or 8, seven be taken as the primary number, thereby excluding the great majority of taxa of the Crassuloideae except species of sect. TILLAEOIDEAE as possible ancestors of the Kalanchoideae. Based on morphology alone, this hypothesis seems doubtful, while the separation between the Kalanchoideae and Cotyledonoideae is based solely on four-merous flowers in the latter subfamily.

The production of plantlets along the margins of leaves by species of *Kalanchoë* sect. BRYOPHYLLUM has attracted the attention of numerous investigators. Stoudt summarized the studies prior to 1938 and pointed out that for all the Crassulaceae investigated, a residual meristem or a secondary "cicatrice" meristem formed from parenchyma cells produces root primordia endogenously and shoot primordia exogenously. Differences in plantlet formation consist of the presence or absence of residual meristems, the location of the meristematic activity, the conditions under which meristematic activity and/or growth of primordia are initiated, and, if residual meristems are present, the degree to which primordia are developed on mature plants. In species of sect. BRYOPHYLLUM, meristematic activity and subsequent growth of plantlets can occur on either attached or detached leaves. In species of sect. KALANCHOË, growth of a new plantlet is apparently induced only when leaves are detached. Moreover, the residual meristematic region in species of sect. KALANCHOË is at the base of the leaf or petiole, not in the crenations of leaf margins.

Numerous studies have attempted to determine the factors that trigger or inhibit the activity of the meristems and the growth and development of the primordia, which in species of *Kalanchoë* are well differentiated when the leaf on which they occur is still immature. The literature concerning this aspect of plantlet production is large, and no attempt has been made to summarize it here. It appears, however, that there are conflicts and contradictions in the literature, and it would be helpful if a plant physiologist could summarize this knowledge; to this end, numerous references are included below.

Because of the ease of propagation of plantlets and the resulting availability of clonal populations, plants of *Kalanchoë* have proven to be apt subjects in experimental studies. Much information concerning the genus has accumulated and is scattered in the physiological literature. For example, it has been determined that *Kalanchoë Blossfeldiana* Poelln. is a typical short-day plant, while *K. crenata*, *K. tubiflora*, and *K. Daigremontiana* are long-short-day plants. Van de Pol (1972) has summarized

available information concerning floral induction and flowering in *Kalanchoë*, and his paper should be consulted for numerous pertinent references of a physiological nature not cited here.

In another study, Groner (1974) has reported that parent plants of *Kalanchoë Daigremontiana* produce a water-soluble allelopathic agent that greatly retards growth (as well as eliciting a syndrome of related characteristics) in daughter plantlets that become rooted within the radius of the parent plant's root system. Groner suggests that this influence is an adaptation for the control of both population size and density. In Madagascar, where the species is native, plantlet production is increased during the rainy season, when it is probable that the plantlets are detached and washed to new areas for establishment. An allelopathic effect was also observed on germination and growth of plants of several other species of monocots and dicots, while others were unaffected, and Groner (1974, 1975) suggests that the allelopathic compound is a unique glycoside, bryophyllosid, recently characterized by Karsten (1965).

No information concerning the breeding system or pollination ecology of *Kalanchoë* has been located, except for the suggestion that flowers of *K. pinnata* are adapted for hummingbird pollination (Knuth, 1908). However, Craft (1942) has described the occurrence of extrafloral nectaries on the uppermost leaves and lowermost floral bracts in *K. pinnata*. These "nectaries" (glandular tissue lying in pitted areas on the lamina) appear and produce droplets high in glucose content only when the plants are in flower.

Several hybrids have been reported in *Kalanchoë*, but all references located refer to hybrids that have arisen either in cultivation or through intentional crosses. A triploid hybrid, $2n = 51$, between *K. Daigremontiana* and *K. tubiflora*, both of sect. Bryophyllum, has been reported by Baldwin (1949) and Warden (1958). Displaying a morphology intermediate between the parental species, the hybrid is apparently well established in American horticulture and is sometimes referred to as *K.* × *hybrida* Hort. Another hybrid has involved *K. Daigremontiana* as the pollen parent and *K. pinnata* as the seed parent, while the intersectional hybrid, *K. Daigremontiana* × *K. Blossfeldiana*, and its reciprocal, have been produced by Resende (1956). Maintaining two genera for the parental species, Resende gave the hybrid group the name × *Bryokalanchoë lisbonensis*, apparently an invalid one lacking a Latin description. Resende's observations on these sterile hybrids indicate that "the capacity to form pseudobulbs is recessive and that SD [short-day] is dominant over LSD [long-short-day]."

Aside from their usefulness in experimental studies, several species of *Kalanchoë* are of economic importance as pot plants. Within recent years numerous cultivars of *K. Blossfeldiana* have been selected and marketed as winter-blooming house plants, and most florist shops offer this species for sale during the Christmas season and into the spring months. Many other species are widely grown by fanciers of succulent plants and may occasionally be found for sale in florist shops.

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THE GENUS PHYLLOCLADUS (PHYLLOCLADACEAE)

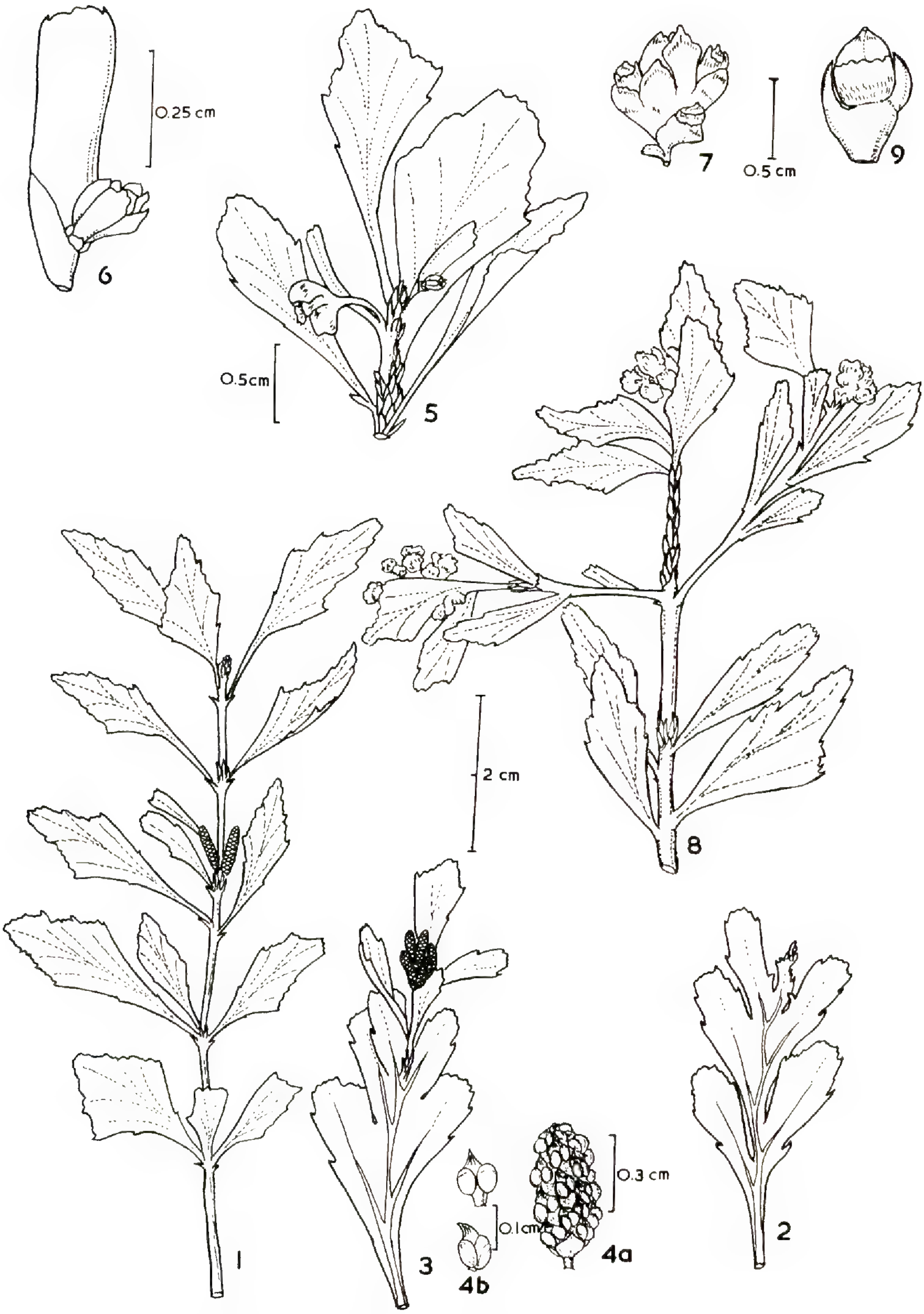
HSUAN KENG

THE CONIFEROUS GENUS *Phyllocladus* (Phyllocladaceae, formerly Podocarpaceae) was established by L. C. and A. Richard in 1826 based on the Tasmanian species *Phyllocladus rhomboidalis* L. C. & A. Rich., and is now known as *P. asplenii folius* (Labill.) Hooker f. (FIGURES 1–9). This genus is noted particularly for the presence of large, celery-leaf-like photosynthetic organs (hence the common names "celery pine" or "celery-topped pine") which have been interpreted as phylloclades and from which the generic name is derived. The prevailing view of the origin and nature of the phylloclades is still dominated by the following statement made by Robertson (1906, p. 259) over half a century ago: "*Phyllocladus* is . . . characterized by the reduction of its true leaves to pointed scales, and the expansion of certain of its stem-branches into flattened leaf-like structures." This implies that the phylloclade is a highly specialized, and therefore an advanced, character.

My previous taxonomic and morphological studies on the genus were based mainly on a single Malesian species, *Phyllocladus hypophyllus* Hooker f. (Keng, 1963a, 1963b). From April to August, 1976, I visited Tasmania and New Zealand, and was able to examine living and preserved material and herbarium specimens of the other known species of *Phyllocladus*. In September and October, 1976, I also visited the Rijksherbarium, Leiden, the Netherlands, and examined a large number of herbarium specimens of *P. hypophyllus* collected from New Guinea and elsewhere in the Malesian regions. The main purpose of this extensive study tour was to re-examine my earlier suggestion (Keng, 1974) that the foliate phylloclade of this genus is a relict feature, possibly derived from or remotely related to the lateral branch systems of the recently established fossil taxon Progymnospermae (or Progymnospermopsida). This was discussed in a paper presented to an I.A.P.T. Symposium in September, 1976, in Hamburg, and has been published elsewhere (Keng, 1977). In this article, the morphology and taxonomy of the genus *Phyllocladus* are discussed, and brief notes on the evolutionary trends and the paleogeographic distribution of the genus are given.

MORPHOLOGY

HABIT. Species of the genus and, in some cases, plants of the same species, range from shrubs or small trees to large trees. *Phyllocladus asplenii folius* var. *alpinus* (previously known as *P. alpinus*) is usually a bushy shrub at high altitudes. Its lowland form, however, may become a small tree, reaching 8–9 meters. *Phyllocladus glaucus* and *P. asplenii folius* var. *asplenii folius* are small to medium-sized trees; the former can attain about 12 meters,



FIGURES 1–9. *Phyllocladus asplenii folius* var. *asplenii folius*: 1, branch bearing whorled simple phylloclades and pollen cones; 2, pinnately lobed phylloclade with terminal bud; 3, young branch with simple phylloclades and pollen cones arising from tip of pinnately lobed phylloclade; 4a, pollen cone; 4b, microsporophyll bearing two pollen sacs (in two views); 5, portion of branch bearing ovulate cones; 6, ovulate cone on side of deformed simple phylloclade; 7, young seed cone; 8, branch bearing mature seed cones; 9, mature seed.

and the latter can reach approximately 18 meters under suitable conditions. The two remaining species, *P. trichomanoides* and *P. hypophyllus*, become lofty trees, reaching a height of approximately 25 and 30 meters, respectively. *Phyllocladus hypophyllus*, however, like most of the other species, becomes stunted in subalpine forests.

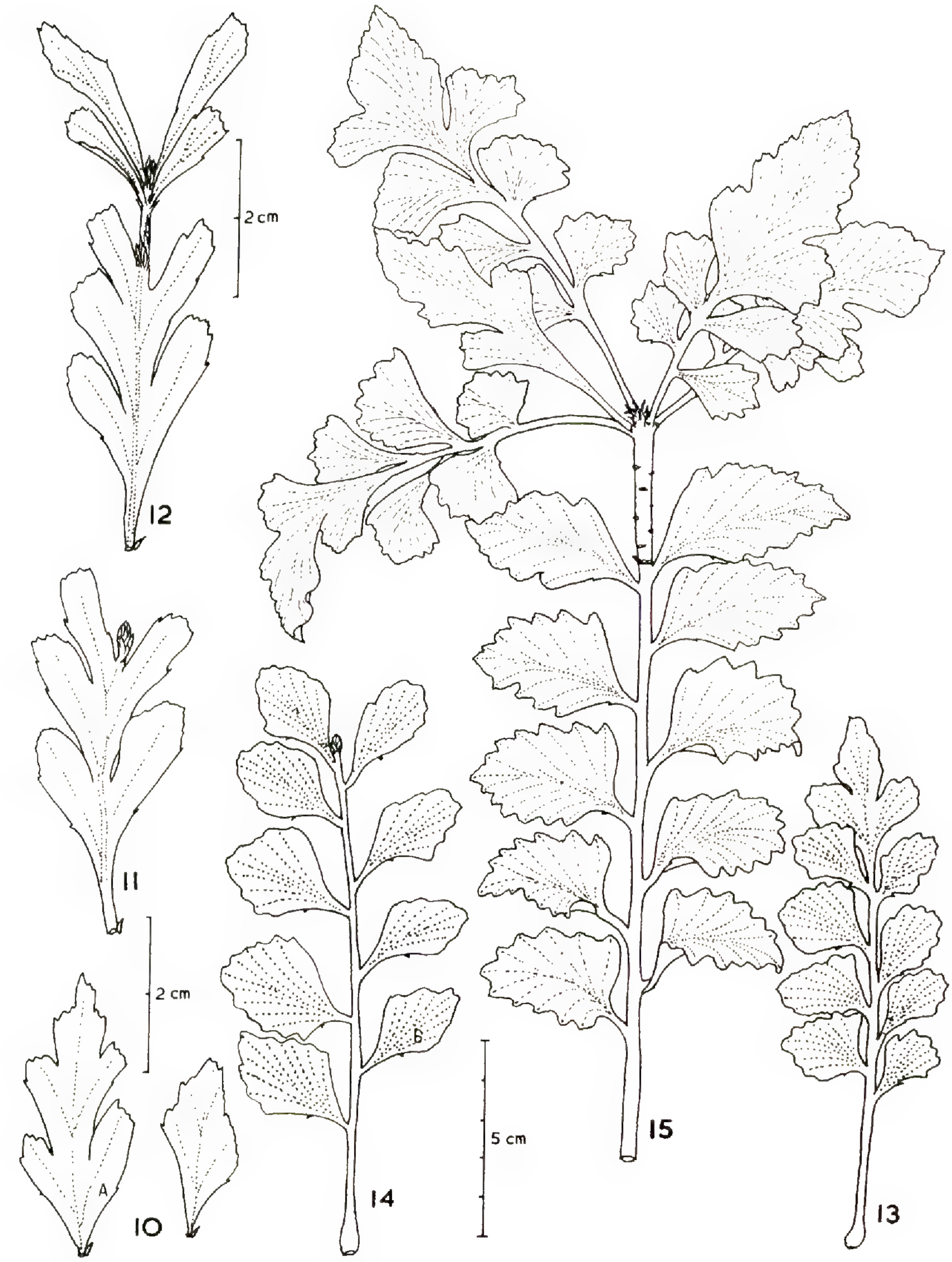
The bark of the species varies from greenish (*Phyllocladus trichomanoides*) to reddish brown (*P. hypophyllus*) or blackish (*P. aspleniifolius* var. *aspleniifolius*), and is yellowish or reddish and fibrous within. It is smooth (e.g., *P. trichomanoides*) or deeply fissured (e.g., *P. aspleniifolius* var. *aspleniifolius*), and is shed in large, thin flakes. Branches and branchlets are borne 3 to 5, rarely 8 or 9, in a false whorl. Trees of *Phyllocladus* can be readily identified in the field by their apparently whorled branches.

Species of *Phyllocladus*, especially *P. aspleniifolius* var. *alpinus*, must be among the slowest growing conifers. A seven-year-old seedling of *P. aspleniifolius* var. *alpinus* in its natural habitat was only 6 cm. tall. It was fully covered with linear juvenile leaves, and one of its two withered cotyledons still persisted. A seedling only 12 cm. tall was estimated to be 25 years old. Trunks of *P. aspleniifolius* var. *alpinus* hardly exceed 30 cm. in diameter, yet may show up to 190 growth rings (Wardle, 1969).

A wild seedling of *P. aspleniifolius* var. *aspleniifolius* of unknown age was brought into cultivation at the Botany Department of the University of Tasmania and, after about 15 years (Prof. W. D. Jackson, University of Tasmania, pers. comm.) has reached a height of 1.1 meters and has begun to produce staminate cones. Displayed at the same department is a large disc of wood with a diameter of about 45 cm. (maximum radius 29 cm., minimum radius 20 cm.). This came from a tree that was cut in 1944 and was estimated by carefully counting the annual rings to be 389 years old.

PHYLLOCLADES (Cladodes). The unique "foliar" organ of the genus is a phylloclade or cladode, which emerges from the axil of an acicular leaf. Phylloclades are alternate, opposite, or more frequently in false whorls on stems and branches. They are thick and leathery, and are extremely variable in shape and size, apparently being easily modified by environmental changes; they can also be quite different in juvenile and adult plants. There are two types of phylloclades: simple phylloclades are found in *Phyllocladus aspleniifolius* var. *aspleniifolius* (FIGURE 10) and var. *alpinus*, while pinnately compound ones are characteristic of *P. glaucus* (FIGURES 13, 14), *P. hypophyllus*, and *P. trichomanoides*.

Simple phylloclades are 1–4 cm. long and are mostly rhombic in outline. Their margins are finely toothed or nearly entire, or sometimes shallowly to deeply 2- to 3-lobed on one or both sides in the lower part. They may also be pinnatifid, but are only very rarely pinnately compound. Some of the pinnatifid phylloclades bear a terminal bud which is covered with awl-shaped scales (FIGURE 11). These buds either remain dormant or give rise to a short shoot usually 1–4 cm. long. These short shoots are spirally covered with short, lanceolate, deciduous leaves, and terminate



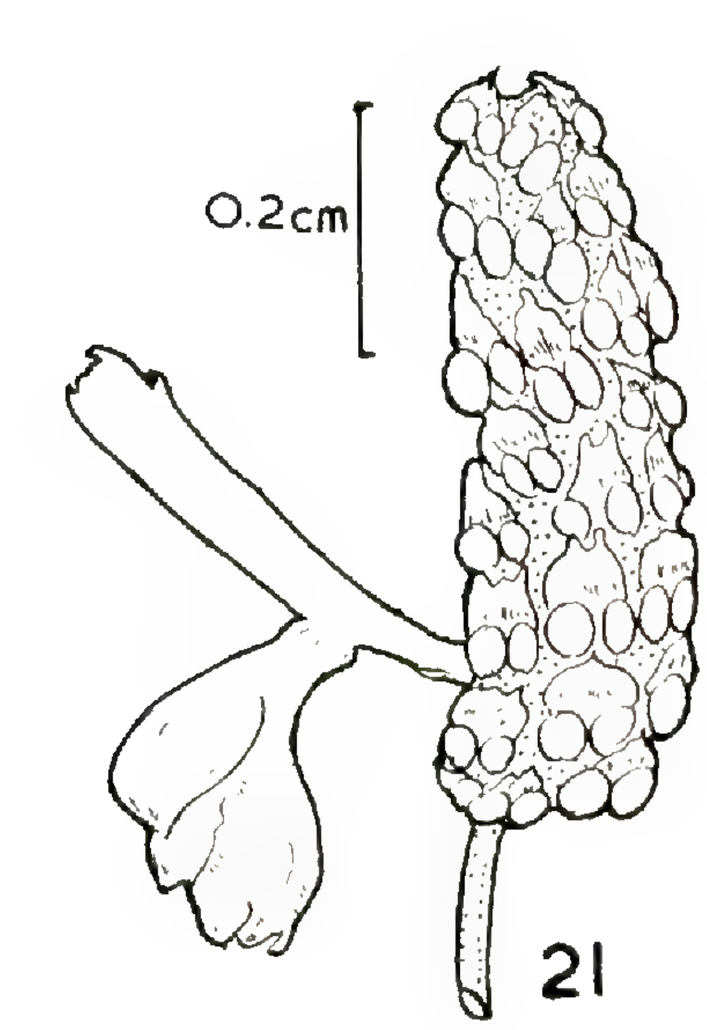
FIGURES 10–15. Simple and pinnately compound phylloclades. 10–12, *Phyllocladus aspleniifolius* var. *aspleniifolius*: 10, two simple phylloclades without terminal bud, one undivided, the other pinnately lobed; 11, simple pinnately lobed phylloclade with terminal bud; 12, short shoot arising from pinnately lobed phylloclade. 13–15, *P. glaucus*: 13, pinnate phylloclade with terminal lobe in place of terminal bud; 14, pinnate phylloclade with terminal bud; 15, short shoot with crown of pinnate phylloclades arising from tip of pinnate phylloclade.

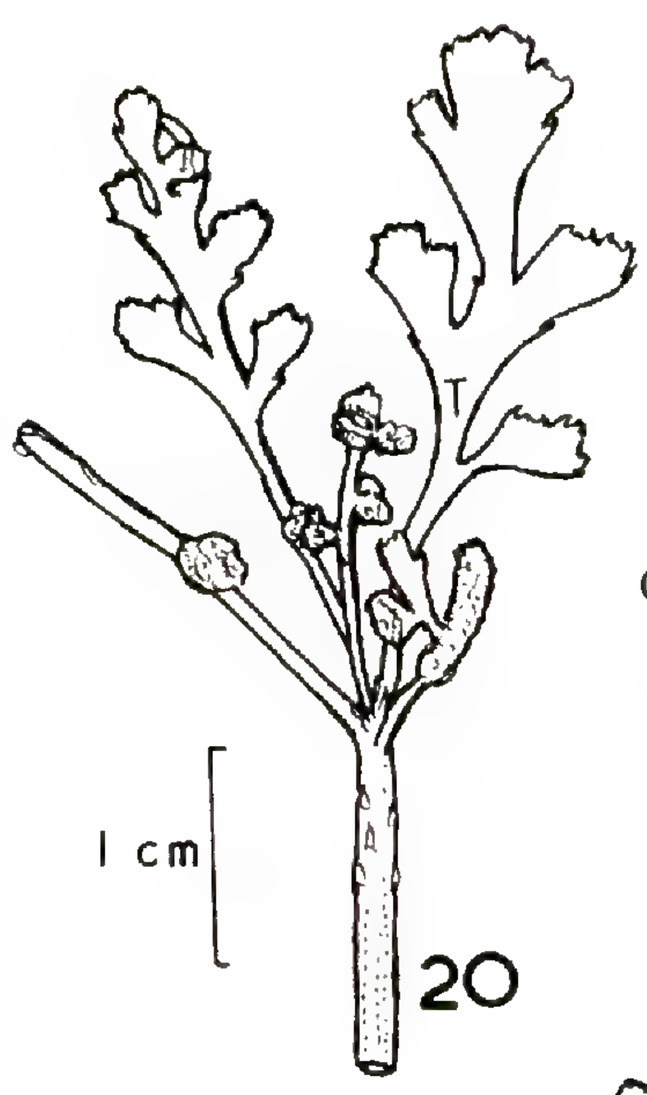
in a group of 3 to 5 simple or occasionally pinnatifid phylloclades with a new terminal bud in the center (FIGURE 12).

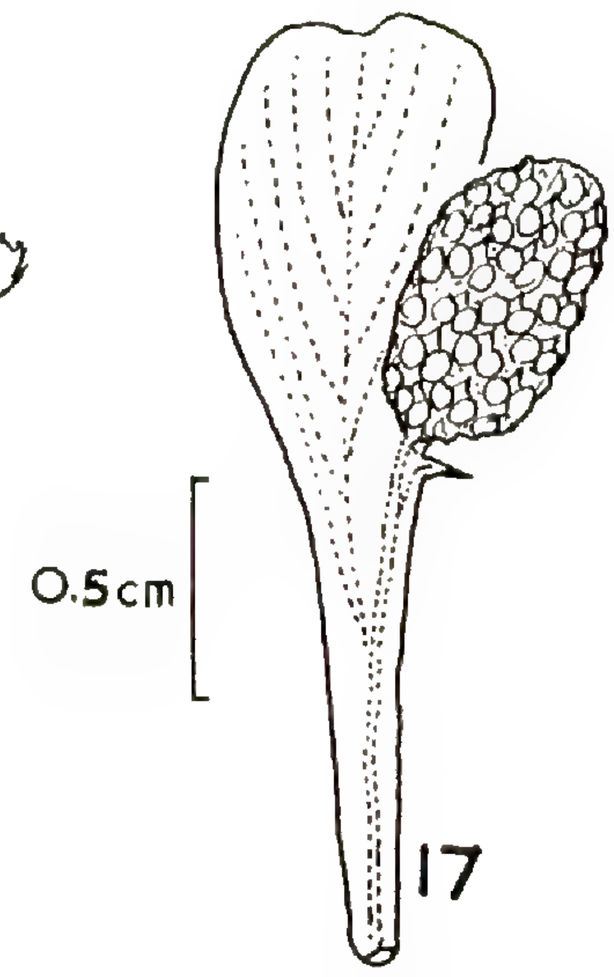
The pinnately compound phylloclades can reach 10–15 cm. in length (in vigorous growth and especially in saplings they may be 30 cm. long), each of them consisting of 5 to 10 (to 12 or more) segments or pinnae distichously arranged in two rows along the rachis. In taxonomic literature these individual segments or pinnae have often been misleadingly called phylloclades or cladodes. The pinnate phylloclades, like the simple ones, may or may not possess a terminal bud (FIGURES 13, 14). In the former case, the terminal bud can develop into a short shoot 4–10 cm. (–15 cm. or more) long. This new short shoot is partly and sparsely covered with deciduous, linear-lanceolate scale leaves and is crowned with 3 to 5 (to 10) normally pinnately compound phylloclades, in addition to a terminal bud (FIGURE 15). In the latter case, there is always a large, prominent terminal segment in lieu of the terminal bud; this terminal segment is often partly lobed or partially fused with one or both lateral segments below it (FIGURE 13).

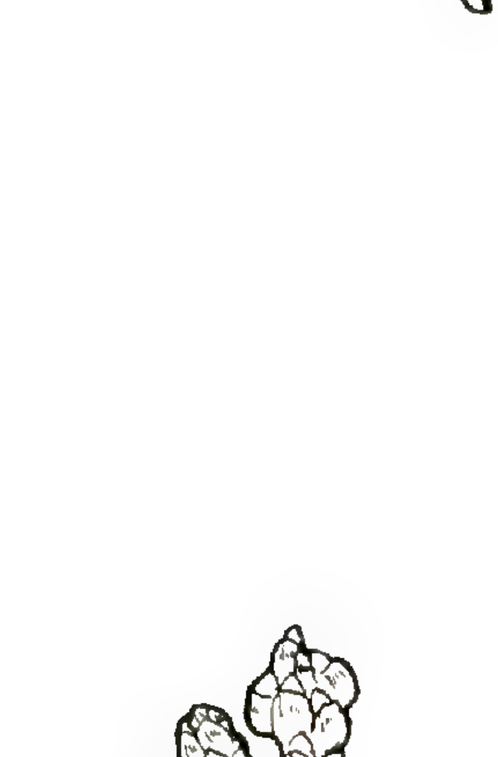
MONOECY AND DIOECY. In taxonomic literature, the same species of *Phyllocladus* has been described as monoecious or dioecious by different authors. For example, *P. asplenii folius* var. *alpinus* was generally considered as monoecious, but Wardle (1969), after careful observation, pointed out that dioecy is the usual condition. It is known that a *Phyllocladus* tree that normally produces pollen cones can occasionally produce a few ovulate cones, although the latter are often aborted to various degrees. Reduced ovulate cones have been found on the same branch with pollen cones in *P. hypophyllus* (Keng, 1962b) (FIGURE 16). Abnormal pollen cones of *P. asplenii folius* var. *alpinus*, each with an ovule at its base, were first reported by Robertson (1906) and again by Wardle (1969). During the present study (FIGURES 20, 21), a well-developed pollen cone was found on a branch of *P. trichomanoides* that bore predominantly ovulate cones. Preserved material of *P. glaucus* collected by Dr. A. E. Orchard from Cranwell Park, Auckland, New Zealand, shows a number of interesting abnormalities. There are 10 to 15 normal pollen cones spirally arranged on the axis of a dwarf shoot, and each is subtended by a lanceolate bract. At the top of the shoot, there are several pinnate phylloclades bearing reduced ovulate cones (FIGURE 18). Some of the pollen cones have reduced ovules at their bases. A most extraordinary teratological specimen from the same collection shows that some of these reduced ovules are in fact subtended by scales in turn bearing two minute pollen sacs.

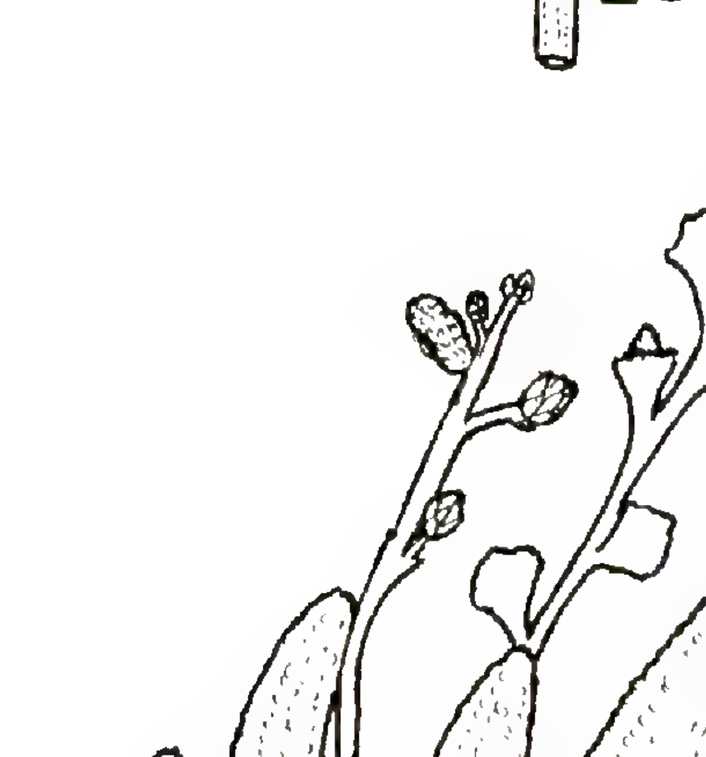
It appears that young trees of most species of *Phyllocladus*, with the possible exception of *P. glaucus*, bear either pollen or ovulate cones and thus are clearly dioecious. When the trees become older, the distinction is less clear. Dr. B. P. J. Molloy of the D.S.I.R., Lincoln, New Zealand, however, believes (pers. comm.) that sexuality of *Phyllocladus* gradually becomes more stable in older trees. Further observation is needed.

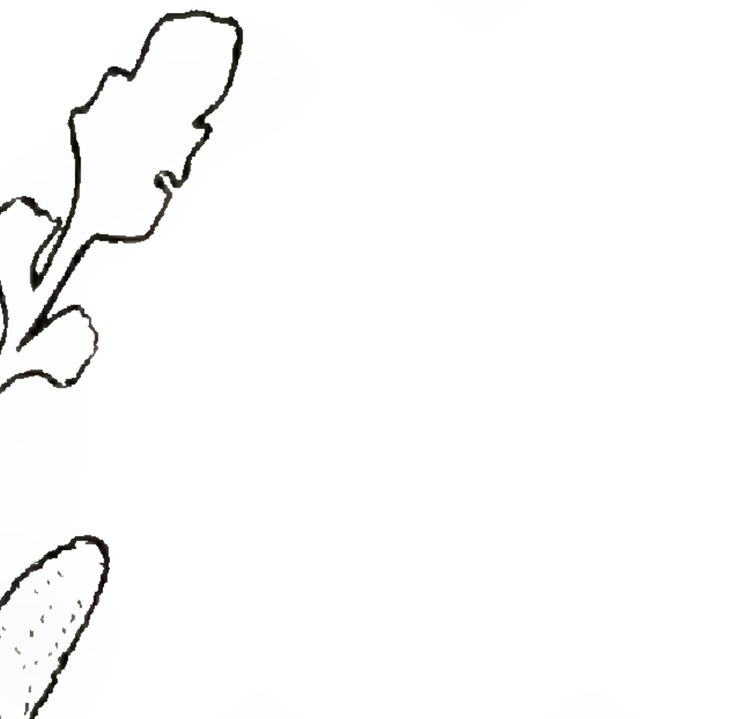








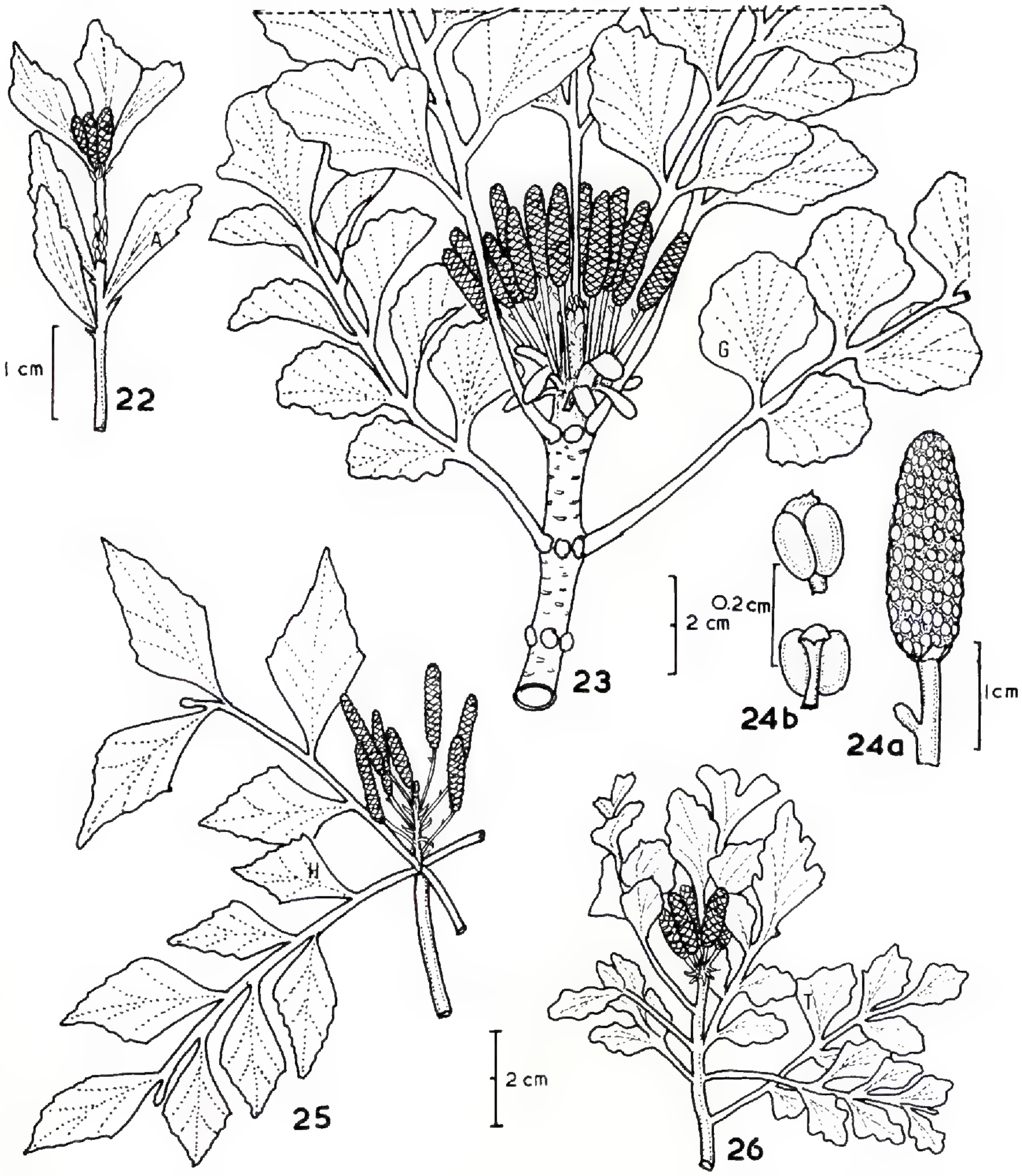




FIGURES 16–21. Some teratological specimens of *Phyllocladus*. 16, 17, *P. hypophyllus*: 16, pollen cones and underdeveloped ovulate cones arising from same branch; 17, pollen cone borne on partly deformed phylloclade. 18, 19, *P. glaucus*: 18, pollen cones spirally arranged on elongate short shoot, with partially reduced ovulate cones above; 19, reduced ovulate cones enlarged, the largest one with ovulate scales concealing aborted pollen sacs beneath. 20, 21, *P. trichomanoides*: 20, branch with ovulate cones and single pollen cone; 21, pollen cone, enlarged.

POLLEN CONES. The pollen cones are nearly sessile or short stalked and are usually crowded on the tip of an unfolding side branch. After the elongation of the new shoot from the tip of a side branch, it becomes apparent that these pollen cones are actually spirally arranged along the axis of the new shoot, and each cone is usually subtended by a bract. Old, dry pollen cones may remain on the tree for months or even years.

The young pollen cones are purplish pink to sulphur yellow in color. There are from 2 to 5 (as in *Phyllocladus asplenii folius* var. *asplenii folius*, FIGURE 22) up to about 20 (as in *P. glaucus*, FIGURE 23) cones together. The pollen cones are cylindrical, 1.5–2 (in *P. asplenii folius*) to 3–4 (in



FIGURES 22–26. Branches of *Phyllocladus* with pollen cones: 22, *P. asplenii folius* var. *asplenii folius*; 23, 24, *P. glaucus* (after T. Kirk); 25, *P. hypophyllus*; 26, *P. trichomanoides*.

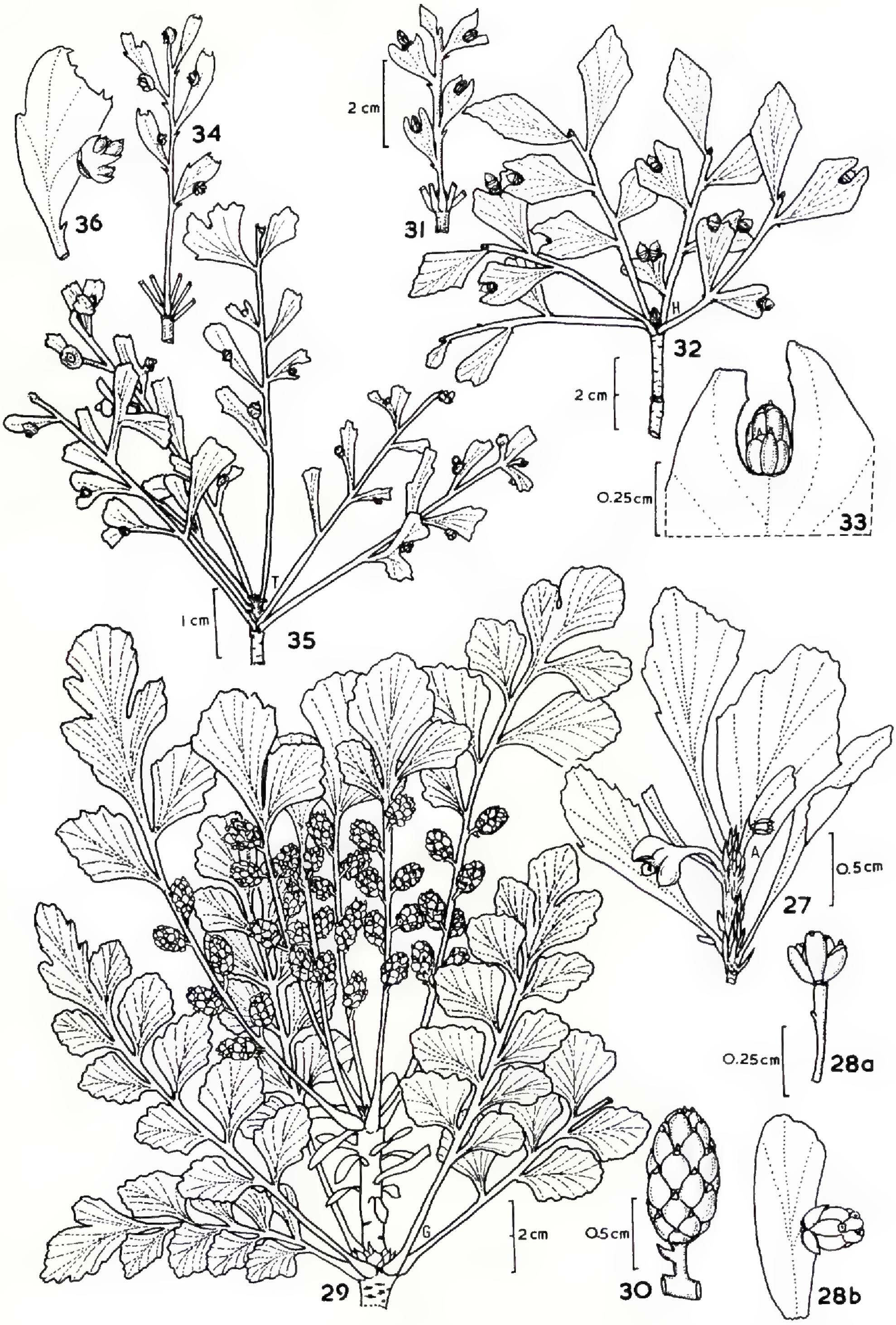
P. glaucus) cm. long, and consist of approximately 30 to 50 (to 60 to 70) cone scales spirally arranged along an axis. The cone scales are triangular in shape, often with a pointed tip and toothed upper margins. Each cone scale bears a pair of pollen sacs at its base (FIGURE 24). The pollen grains have two tiny bladder wings and are dispersed by wind.

The stalk of the pollen cone is always associated with a bractlike structure. From observation of teratological specimens of *Phyllocladus hypophyllus* (Keng, 1963b, 1974) (FIGURE 17) and other species, it was suggested that the bractlike structure on the stalk might represent a much-reduced simple phylloclade. It probably means that the pollen strobili were originally borne at the end of a simple phylloclade (or on the segments of a pinnate phylloclade). A similar situation still occurs in the ovulate strobili of modern species.

OVULATE CONES. In the species with simple phylloclades (i.e., *Phyllocladus aspleniifolius* var. *aspleniifolius* (FIGURE 27) and var. *alpinus*), the ovulate cones are single or borne 2 to 4 together. They arise below or on one side of a slightly deformed cladode (FIGURE 28, b), or are apparently terminal on a long stalk (FIGURE 28, a), the entire cladode being reduced. In species with pinnate phylloclades (*P. glaucus, P. hypophyllus*, and *P. trichomanoides*), the ovulate cones are either seated in the notch of a bilobed segment (e.g., *P. hypophyllus*) (FIGURES 31, 32) or attached to both sides of the rachis of a pinnate cladode, occupying the place of the lower lateral segments (e.g., *P. glaucus*) (FIGURE 29). Although these are the normal situations, there is considerable variation. For example, in *P. hypophyllus* the notched segments may be reduced to various degrees while the main axis of a pinnate cladode becomes enlarged and columnar; in *P. trichomanoides* (FIGURES 34, 35), on the other hand, the segments underneath the ovulate cones often become deformed or almost obsolete.

The ovulate cones are sessile (e.g., *Phyllocladus hypophyllus*) (FIGURE 33) or short stalked (e.g., *P. glaucus*) (FIGURE 30). They are usually ovoid in outline and consist of few to many, more or less spirally arranged cone scales. Some of these scales (usually 2 or 3, sometimes more) possess a single axillary ovule; most of the others, however, are barren. In most species, normally only one (rarely two or three) ovule in an ovulate cone develops into a seed, but in *P. glaucus* a fair number of seeds (5 to 10, sometimes up to 20) are produced in a single cone.

SEEDS. The seeds are oval in shape, slightly compressed dorsiventrally, and pointed above, often with a tiny, crooked tip. They are generally very small. Among the four species, *Phyllocladus trichomanoides* has the smallest seeds (2–3 mm. long), and *P. hypophyllus* the largest (6–8 mm. long). A conspicuous, cup-shaped aril protrudes beyond the ripe cone scales and envelops the lower half or two-thirds of the seed (FIGURE 9). The aril is more or less symmetrical, but the upper edge is often dentate or irregularly lobed. Mature cone scales are fleshy or leathery, and more or less fused. The cone scales form an amorphous mass known as the "receptacle" in the species with fewer cone scales; in *P. glaucus* the cone scales remain dis-



FIGURES 27–36. Branches of *Phyllocladus* with ovulate and seed cones. 27, 28, *P. asplenii folius* var. *asplenii folius*: 27, branch with both ovulate and young seed cones; 28, a, b, two ovulate cones, one subtended by phylloclade, the other appearing terminal. 29, 30, *P. glaucus*: 29, branch with seed cones borne on lower part of pinnate phylloclades (after T. Kirk); 30, ovulate cone. 31–33, *P. hypophyllus*: 31, ovulate cone in notches of pinnae of pinnate phylloclade; 32, branch with seed cones in notches of pinnae of pinnate phylloclades; 33, ovulate cone. 34–36, *P. trichomanoides*: 34, ovulate cones on one side of pinnae of pinnate phylloclade; 35, branch with seed cones; 36, ovulate cone.

tinguishable, and are more numerous (to about 20). Fully ripened scales usually turn bright red, in sharp contrast to the colors of the aril and seed, the former normally being white and the latter either chestnut brown (as in *P. hypophyllus*) or black (as in *P. asplenii folius* and others). The mature seeds fall from the arils to the ground close to the parent tree. However, due to the highly contrasting colors of the seed, the aril, and the receptacle, as well as the small size of the seed, it is conceivable that the seed of *Phyllocladus* might also be dispersed by birds as suggested by Preest (1963).

SEEDLINGS. The two cotyledons (FIGURE 37) are usually early deciduous but may last for two to several years before turning brown and withering away; they always leave a pair of inconspicuous scars on the lower part of the axis. They are linear-lanceolate in shape, double-nerved, 1.5–2 cm. long, and shallowly notched or bilobed at the apices. The juvenile leaves are linear and single-veined, varying between 0.5 and 1 cm. in length. They are spirally arranged on the axis. Their apices are acute or rounded and are often sharp pointed at the extremity. Later-produced leaves become successively smaller, finally being lanceolate or triangular scale leaves usually 2–3 mm. long; phylloclades or cladodes are present in the axils of some of these scale leaves. In *Phyllocladus asplenii folius* (FIGURE 38), the cladodes on seedlings are mostly simple, although toothed or crenate to various degrees in the margins. In *P. hypophyllus* (FIGURES 40, 41), the earlier-formed cladodes are simple; these are gradually replaced by the deeply lobed ones. The lobation then becomes more pronounced until, finally, almost all the cladodes are pinnately compound. In *P. glaucus* (FIGURE 39) and *P. trichomanoides* (FIGURES 42, 43), even the earlier-formed cladodes are pinnatifid. In the latter species, the cladodes of a fully grown seedling are distinctly pinnate and with the pinnae further shallowly or deeply lobed, thus approaching a bipinnate state (FIGURE 43).

The color of the seedlings varies from green (*Phyllocladus asplenii folius*), to grayish green (*P. glaucus*, *P. hypophyllus*), to purplish (*P. trichomanoides*), but this also depends on environmental conditions. Seedlings of nearly all species of *Phyllocladus*, especially those of *P. asplenii folius* var. *asplenii folius* and var. *alpinus*, are highly polymorphic with respect to the shape, size, and dentation of the early-formed cladodes. This probably suggests that they are not homogeneous genetically.

Dr. R. K. Crowden, of the University of Tasmania (pers. comm.), points out that in Tasmania, where forest fires are comparatively frequent, *Phyllocladus asplenii folius* var. *asplenii folius* is well adapted for survival. Seeds of this plant can probably remain in the forest soil for several years. After a forest fire, the vegetation is largely devastated, but a great number of seedlings of *Phyllocladus* often appear in the burned-over area. In contrast to this, seeds of the New Zealand species appear to be very short lived (Dr. B. P. J. Molloy, pers. comm.).

Seedlings of all the *Phyllocladus* species observed possess root nodules which contain symbiotic, nitrogen-fixing bacteria. These nodules are

especially well developed in the Tasmanian and New Zealand species. This is probably one of the attributes that enable the seedlings to survive in a rather unfavorable environment.

EVOLUTIONARY TRENDS

The following hypothetical evolutionary trends seem to occur within the genus *Phyllocladus*. In the trends listed, the simpler condition is considered to be the derived state; the more complex condition, the ancestral.

PHYLLOCLADES. The seemingly bipinnate phylloclades, as seen in the seedlings of *Phyllocladus trichomanoides* (FIGURE 43), likely represent the ancestral form from which simple pinnate, pinnatifid, and finally simple phylloclades (as in *P. aspleniifolius*, FIGURE 10) were probably evolved.

POLLEN STROBILI. Each pollen strobilus was probably originally seated in the top notch of a simple phylloclade, as shown in a teratological specimen of *Phyllocladus hypophyllus* (FIGURE 17). These simple phylloclades are usually either reduced and bractlike (FIGURE 24, a) or obsolete. In *P. glaucus*, there are numerous (about 20) long-stalked, bracteate strobili, each composed of many (approximately 60 to 70) sporophylls. These strobili first appear to be crowded on the top of a short shoot and to surround the terminal bud (Figures 23, 26); later, after the activation of the terminal bud and the elongation of the new short shoot, it becomes clear that they are actually spirally arranged on the new short shoot (FIGURES 18, 25). In contrast, *P. aspleniifolius* var. *aspleniifolius* (FIGURES 1, 3, 4) has only 2 or 3 almost sessile strobili, with each strobilus composed of only 30 to 50 sporophylls. The latter probably represents the most highly evolved form.

OVULATE STROBILI. Each strobilus was probably originally seated in the notch of a pinna of a pinnate phylloclade, as shown in *Phyllocladus hypophyllus* (FIGURES 31, 33) and in some cases also in *P. trichomanoides* (FIGURE 35). These pinnate phylloclades thus remarkably and uniquely perform both vegetative and reproductive functions. There are 4 or 5 or more strobilus-bearing pinnate phylloclades together, arranged on the top of a short shoot in a false whorl. Each strobilus, presumably in the basic form, consists of a large number (to 20 or so) of fertile scales, as seen in *P. glaucus* (FIGURE 30).

DISTRIBUTION OF SEXES. The trend seems to be from monoecious to dioecious. Nearly every species of *Phyllocladus* shows a certain degree of monoecism. The ancestral form probably possessed a number of simple phylloclades spirally arranged on a short shoot, each of which bore a terminal staminate strobilus. On the tip of the same short shoot, there was a crown of pinnate phylloclades, each with an ovulate strobilus on its pinna (cf. FIGURE 18).

In short, among the four living species, it appears that *Phyllocladus glaucus* probably preserves more primitive traits than do the other species. This species is followed by *P. hypophyllus* and *P. trichomanoides*. Con-

FIGURES 37–43. Seedlings of *Phyllocladus*: 37, 38, *P. asplenii folius* var. *asplenii-folius*; 39, *P. glaucus*; 40, 41, *P. hypophyllus*; 42, 43, *P. trichomanoides*.

versely, *P. aspleniifolius* var. *aspleniifolius* and var. *alpinus* in many respects possibly represent the much-reduced or the highly evolved form.

TAXONOMIC TREATMENT

Phyllocladus L. C. & A. Richard, Comment. Bot. Conif. Cycad. 129. *t. 3, fig. 12.* 1826.

Podocarpus Labill. Nov. Holl. Pl. Sp. **2:** 71. *t. 221.* 1806, non L'Hérit. ex Pers.
Brownetera L. C. Rich. Ann. Mus. Hist. Nat. Paris **16:** 299. 1810, *nomen nudum.*
Thalamia Sprengel, Anl. Kennt. Gewächse. ed. 2. **2:** 218. 1817.

Shrubs or small to large trees. Juvenile leaves at first linear, changing gradually to subulate and scaly. Phylloclades simple, pinnatifid, or pinnately compound, variable in shape and size, usually 2 to 5 or more in a false whorl. Plants with unisexual strobili mostly dioecious, sometimes monoecious. Pollen cones 2 or 3 (up to 20), crowded in a cluster on the top of a short shoot, becoming spirally arranged along the new short shoot after its elongation; individual pollen cones consisting of 30 to 70 spirally arranged sporophylls, each bearing 2 pollen sacs; pollen grains winged. Ovulate cones terminal or marginal on fully grown or reduced simple phylloclades, or on the pinnae of a pinnate phylloclade, the phylloclades 2 to 5 or more in a false whorl on the top of a short shoot; individual ovulate cones consisting of few, several, or numerous scales, usually only one or few, sometimes many (as in *Phyllocladus glaucus*) of the scales being fertile; ovules erect, solitary in the axil of a scale. Seeds ovoid, dorsiventrally compressed, subtended by a cup-shaped, filmy aril and the often fused, succulent scales.

Four species, distributed in Tasmania, New Zealand, and Malesia (from New Guinea to Luzon and Borneo).

TYPE SPECIES: *Phyllocladus rhomboidalis* L. C. & A. Richard (= *Phyllocladus aspleniifolius* (Labill.) Hooker f.).

KEY TO THE SPECIES OF PHYLLOCLADUS

A. Phylloclades of adult plants mostly simple, sometimes shallowly or deeply lobed, occasionally pinnatifid, very rarely truly pinnate. [Ovulate cones solitary or 2 to 4 on the margins and base of a modified (often much-reduced, with the cones thus seeming to be terminal) phylloclade, usually two or more such modified or reduced phylloclades together in a small cluster.] . . . . . 1. *P. aspleniifolius.*

A. Phylloclades of adult plants always pinnate, consisting of 5 or 6 to many (about 12) distinct segments.

B. Ovulate cones normally seated in the apical notch of a segment of the phylloclade, the segment varying from obcordate to oblanceolate, sometimes columnar, very rarely totally reduced; mature seeds 5–8 mm. long, mostly solitary, rarely in pairs, in an ovulate cone. . . . . 3. *P. hypophyllus.*

B. Ovulate cones usually on the margins and base of a segment which is often highly modified (the lower segments in a pinnate phylloclade sometimes

totally reduced, the ovulate cones thus appearing to be terminal on a side branch of the rachis); mature seeds 2–4 mm. long, 1 to many per cone.

C. Ovulate cones consisting of about 10 to 20 fertile scales; mature cones 1 or rarely 2 seeds; pollen cones 5 to 10 terminating a branchlet. . . . . 2. *P. glaucus.*

C. Ovulate cones consisting of 2 or 3 fertile scales; mature cones with 1 or rarely 2 seeds; pollen cones 5 to 10 terminating a branchlet. . . . . 4. *P. trichomanoides.*

1. **Phyllocladus aspleniifolius** (Labill.) Hooker f. in London Jour. Bot. 4: 151. 1845.

Podocarpus aspleniifolia Labill. Novae Holl. Pl. Sp. **2:** 71. *t. 221.* 1806. TYPE: Tasmania, *J.-J. H. de Labillardière* (not seen).

Phyllocladus rhomboidalis L. C. & A. Rich. Comment. Bot. Conif. Cycad. 23. *t. 3, fig. 2.* 1826.

Phyllocladus billardieri L. C. Rich. ex Mirbel in Mém. Mus. Hist. Nat. Paris **13:** 48. 1825, *nomen nudum.*

Thalamia aspleniifolia (Labill.) Sprengel, Anl. Kennt. Gewächse. ed. 2. **2:** 218. 1817.

Shrub or small to medium-sized tree, 6–18 m. high. Bark brownish to dark brown, deeply furrowed in old trees. Juvenile leaves on seedlings linear, 0.7–1 cm. long. Scale leaves on seedlings and on the short branches of adult plants triangular or subulate, 0.1–0.3 cm. long. Phylloclades on seedlings usually linear-oblong to rhomboid, 1.5–2.5 cm. by 1–1.2 cm., shallowly or deeply lobed, sometimes pinnatifid; phylloclades on adult plants mostly simple, rhomboid, 2.5–8 cm. by 1.5–2 cm., the apex acute or blunt, the base cuneate, sessile or stalked, the margins irregularly lacerate or occasionally pinnatisect, very rarely pinnately compound. Plants usually dioecious. Pollen strobili usually 2 or 3 (to 5) together, terminating lateral branches, cylindrical, 0.3–0.5(–1) cm. long, sulphur yellow, short stalked. Ovulate strobili solitary or several (2 to 4) at the side or base of a modified or highly deformed phylloclade, or sometimes the latter totally reduced, with 2 to 4 ovulate strobili together forming a seemingly terminal stalked cluster, each strobilus consisting of 2 or 3 (to 5) erect ovules each subtended by a pinkish red, fleshy scale. Seeds ovoid, about 0.5 cm. long, greenish black to black; aril white, irregularly lobed; receptacle purplish red and fleshy.

KEY TO THE VARIETIES OF PHYLLOCLADUS ASPLENIIFOLIUS

A. Shrub or small to medium-sized tree, maximum height about 18 m.; scale leaves on short shoots of adult plants subulate, 0.2–0.3 cm. long. Confined to Tasmania. . . . . 1a. var. *aspleniifolius.*

A. Shrub or small tree, maximum height about 9 m.; scale leaves on short shoots of adult plants triangular, less than 0.1 cm. long. Restricted to New Zealand. . . . . 1b. var. *alpinus.*

1a. Phyllocladus aspleniifolius (Labill.) Hooker f. var. aspleniifolius.

FIGURES 1–9.

Phyllocladus aspleniifolius (Labill.) Hooker f. in London Jour. Bot. **4**: 151. 1845; Henkel & Hochst. Synop. Nadelhölzer, 371. 1865; Pilger in Engler, Pflanzenr. **4**(5): 97. 1903; Curtis in Stones, Endemic Fl. Tasmania **3**: 106. *pl. 60*. 1971; Curtis & Morris, Stud. Fl. Tasmania. ed. 2. **1**: 2. *fig. 2*. 1975.

Phyllocladus rhomboidalis L. C. & A. Rich. Comment. Bot. Conif. Cycad. 23. *t. 3, fig. 2*. 1826; Endlicher, Synop. Conif. 235. 1847; Hooker f. Fl. Tasmaniae (Bot. Antarctic Voy. pt. 3) **1**: 358. 1859; Carrière, Traité Gén. Conif. ed. 2. 706. 1867; Parlatore in DC. Prodr. **16**(2): 499. 1868; Curtis, Stud. Fl. Tasmania **1**: 234. 1956.

Phyllocladus billardieri L. C. Rich. ex Mirbel in Mém. Mus. Hist. Nat. Paris **13**: 48. 1825, *nomen nudum*.

Phyllocladus serratifolia Nois. ex Henkel & Hochst. Synop. Nadelhölzer, 372. 1865.

Podocarpus aspleniifolia Labill. Novae Holl. Pl. Sp. **2**: 71. *t. 221*. 1806.

Thalamia aspleniifolia (Labill.) Sprengel, Anl. Kennt. Gewächse. ed. 2. **2**: 218. 1817.

This variety is characterized by its taller stature (maximum height about 18 m.) and by its longer (about 0.2–0.3 cm.) subulate scale leaves on the short shoots of adult plants.

DISTRIBUTION. Endemic to Tasmania, Australia (MAP 1). In temperate rain and wet sclerophyll forests, from 500 to 800 meters, largely confined to the western or the moist parts, occasionally descending to sea level in wet coastal areas.

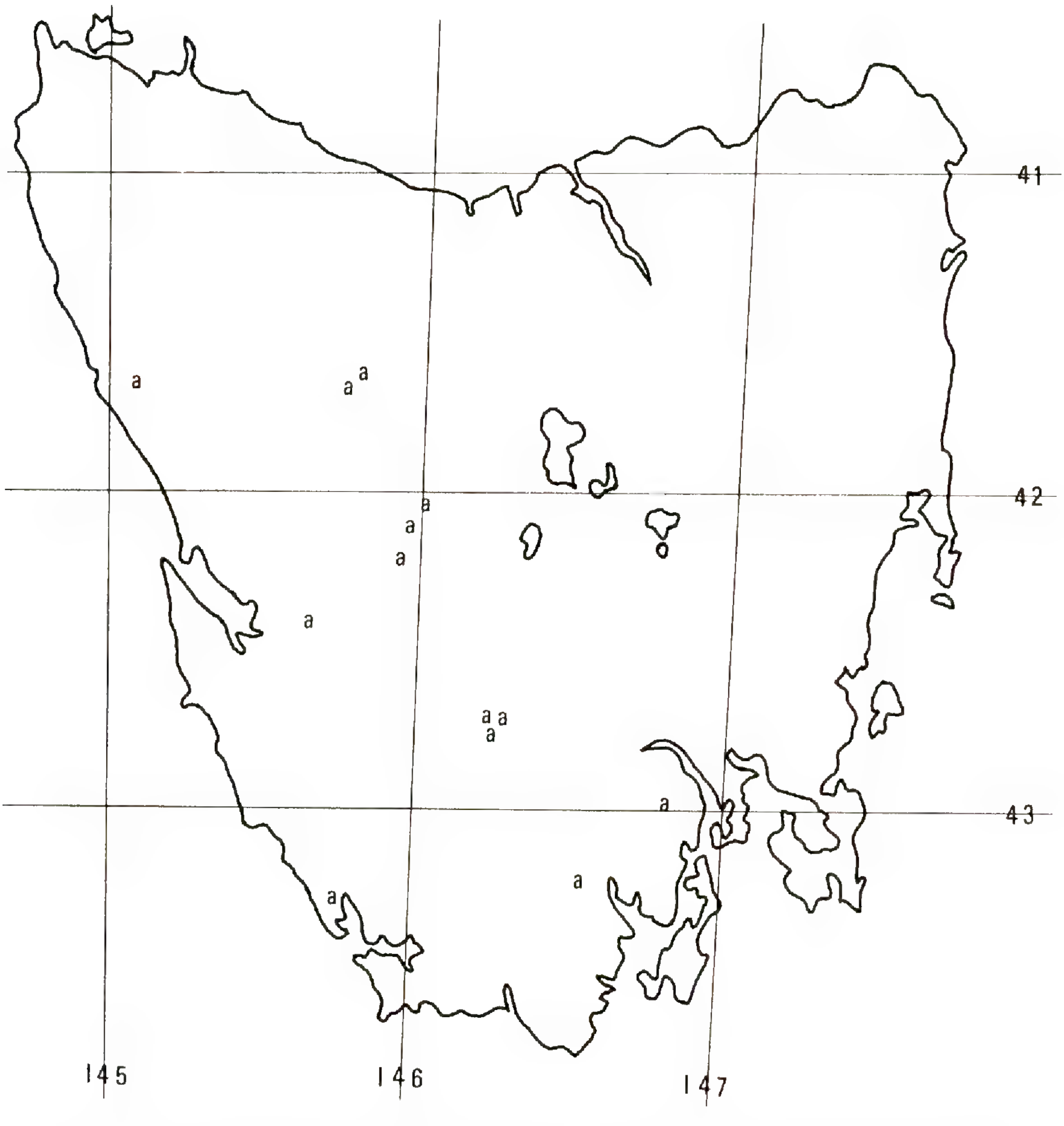
REPRESENTATIVE SPECIMENS. **Australia.** TASMANIA: Corinna, *W. D. Jackson, J 146* (HO *2775*); Cradle Mts., *N. Sunderland* (HO *2776*); Lake St. Clair, below Mt. Ida, *N. T. Burbidge* (HO *2768*); King William Range, *E. Rodway 134* (HO *2767*); Mt. Field Nat. Park, *H. D. Gordon* (HO *2756*); *W. M. Curtis* (HO *2751*); Wishing Well, Mt. Wellington, *J. Somerville* (HO *2766*); Huon River, near Picton Hut, *Somerville 288* (HO *2806*); near Franklin Bridge, Lyell Highway, *J. Townrow* (HO *2782, 2801*); Port Davey, *D. H. Martin* (HO *2777, 2778*).

1b. Phyllocladus aspleniifolius (Labill.) Hooker f. var. alpinus (Hooker f.) H. Keng, comb. nov.

Phyllocladus alpinus Hooker f. Fl. Novae-Zeland. **1**: 235. *t. 53*. 1853; Carrière, Traité Gén. Conif. ed. 2. 708. 1867; Kirk in Trans. New Zealand Inst. **10**: 382. 1878, Forest Fl. New Zealand, 199. *t. 100*. 1889; Pilger in Engler, Pflanzenr. **4**(5): 98. 1903; Cheeseman, Man. New Zealand Fl. 659. 1906, ed. 2. 120. 1925; Allan, Fl. New Zealand **1**: 112. 1961; Wardle in New Zealand Jour. Bot. **7**: 76. 1969. TYPE: New Zealand. North Island, Tongariro, *Bidwill*.

Phyllocladus trichomanoides D. Don var. *alpinus* (Hooker f.) Parl. in DC. Prodr. **16**(2): 498. 1868.

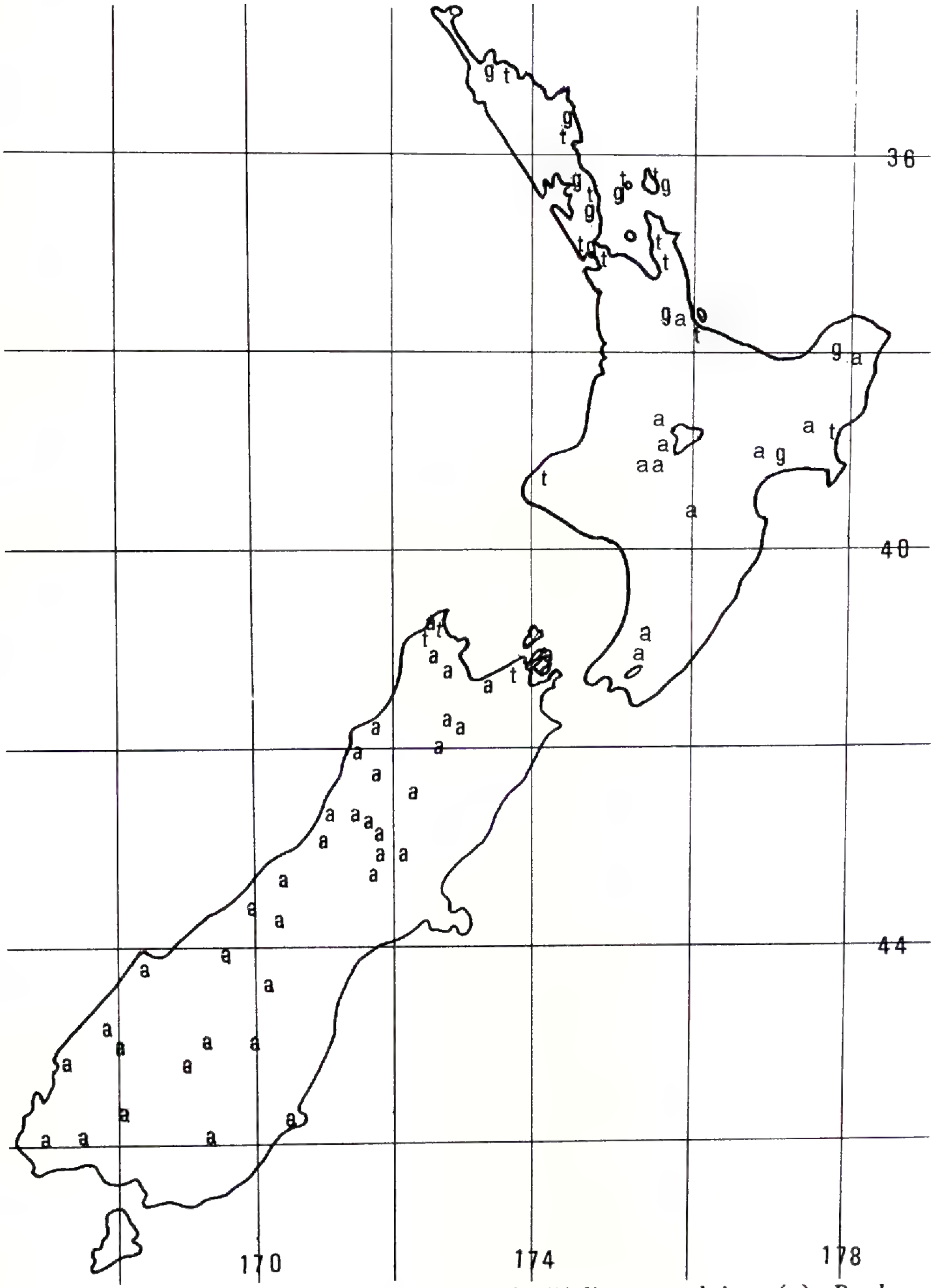
This variety differs from the typical form of the species in the lower stature (maximum height about 9 m.) and in the shorter (less than 0.1 cm.) triangular scale leaves on the short shoot in adult plants.



MAP 1. Distribution of *Phyllocladus asplenifolius* var. *asplenifolius* in Tasmania, Australia.

DISTRIBUTION. Endemic to New Zealand (MAP 2). In montane and subalpine forests and scrubs, usually at 500 to 1900 meters altitude on both North and South Islands, extending from approximately 37 degrees latitude to Foveaux Strait, but descending to sea level to the west of the coastal mountains of Nelson, the Southern Alps, and south of Southland.

REPRESENTATIVE SPECIMENS. **New Zealand.** NORTH ISLAND: King County, Pureora, *T. W. Rawson* (CHR *56455*); Coromandel Peninsula, Moehau, *L. B. Moore* (CHR *40942*, *40943*); Raukumara Range, Hikurangi, *I. R. Fryer* (CHR *185456*); Almateatua, Maungaha-rutu Range, *A. N. Druce* (CHR *216842*); Volcanic Plateau, Puke-o-nake, *P. Wardle* (CHR *185468*); Tongariro Nat. Park, Chateau, *R. Mason* (CHR *82609*); Ruapehu Nat. Park, *A. Cook* (CHR *69111*); Central Ruahine Range, near Waikanaka Hut, *Wardle* (CHR *185459*); Ararua Range, *Druce* (CHR *190505*, *190506*); Wellington, Wilton's Bush, *Harrigan & Cook* (CHR *83778*). SOUTH ISLAND: Nelson, Wanagapeka River, *B. H. MacMillan* (CHR *219942*); Cobb Valley, Sylvester Stream, *Moore* (CHR *151027*); near



MAP 2. Distribution of *Phyllocladus asplenii folius* var. *alpinus* (a), *P. glaucus* (g), and *P. trichomanoides* (t) in New Zealand.

Nelson, Dun Saddle, *Wardle* (CHR *179033*); Marlborough, Mt. Stokes, *J. G. Hay* (CHR *112278*); Lewis Pass, Paradise Lake, *A. H. MacRae* (CHR *185463*); near Agnes Bivouac, Clyde River, *D. R. Given* (CHR *178859*); Arthur's Pass, *R. Melville* (CHR *130873*); Mt. Cook, Hermitage, *H. E. Connor* (CHR *108109*); Mt. Cockayne, Broken River, *E. M. Chapman* (CHR *258592*); Karangama,

Westland Nat. Park, *Wardle* (CHR *179110*); fiords, Stuart Mts., *W. H. Thomson* (CHR *88133*); Expectation Stream, Caswell Sound, *V. D. Zotov* (CHR *71084*); Fiordland, Lake Make, *M. J. A. Simpson* (CHR *115975*); Southland, Nevis, *A. J. D. Barker* (CHR *20950*); Matukituki, Otago, *J. A. Langbein* (CHR *167031*); N. Otago, Omarama, *Moore* (CHR *71226*); Lake Ohau, Dobson River, *Wardle* (CHR *185470*).

In his *Flora Tasmaniae* (Vol. 1, p. 359), J. D. Hooker commented that the New Zealand alpine species (*Phyllocladus alpinus*) so closely resembles the Tasmanian species that he almost doubted "its being distinct." T. Kirk (in Trans. Proc. New Zealand Inst. 10: 382, 383. 1878) stated that "I have no doubt that it [*P. alpinus*] will ultimately prove identical with the Tasmanian *P. rhomboidalis*, . . . for although specimens from alpine habitats look very different to that plant, fruited specimens from low levels are undistinguishable." Recently, P. Wardle (1969) recognized two ecotypes (alpine and lowland) of this plant and observed that the lowland ecotype of *P. alpinus* is very similar to the Tasmanian plant. He also mentioned three characters that distinguish them: maximum height, bud scales in the adult plant, and seed clusters. The last character (seed clusters usually lateral at the base of the phylloclade in New Zealand species and usually terminal on the phylloclade in Tasmanian plants) does not stand, so varietal rank seems most appropriate.

2. **Phyllocladus glaucus** Carr. Traité Gén. Conif. 502. 1855, ed. 2. 707. 1867; Kirk in Trans. New Zealand Inst. 1: 149. 1868, *ibid.* 10: 380. 1878, Forest Fl. New Zealand, 195. *tt. 98, 99*. 1889; Pilger in Engler, Pflanzenr. 4(5): 95. 1903; Cheeseman, Man. New Zealand Fl. 658. 1906, ed. 2. 120. 1925; Allan, Fl. New Zealand 1: 113. 1961. TYPE: New Zealand. North Island, Maungatawhiri, *R. Mair*.

Phyllocladus trichomanoides D. Don var. *glaucus* (Carr.) Parl. in DC. Prodr. 16(2): 498. 1868.

Small tree, to 12 m. tall. Bark dark brownish, deeply fissured. Juvenile leaves on seedlings linear, obtuse or acute, sometimes falcate, 0.5–1 cm. long. Scale leaves on seedlings subulate, about 0.5 cm. long; those at the base of a young terminal shoot of adult plant linear-lanceolate, 1.5–2 cm. long, thin-membranaceous, caducous. Phylloclades on seedlings usually deeply pinnatifid, 3–5 cm. long; those on adult plants pinnately compound, 12–20(–30) cm. long, consisting of 5 to 10 (to 12) segments, the segments pale bluish green above and glaucous beneath when young, rhombic to ovate-flabellate, 2–5 cm. long, subsessile or stalked. Plants usually dioecious. Pollen strobili usually 10 to 20 crowded at the tips of the short branches, cylindrical, 1–2(–2.5) cm. long, stalked, the stalk stout, equaling or longer than the cone. Ovulate strobili 3 to 5, inserted on each side of the pinnate phylloclades at the tips of the short branchlets, occupying the place of the lower lateral segments; each strobilus ovoid, 0.5–0.8 cm. long, consisting of 10 to 20 spirally arranged fertile scales. Ripe seed cones pinkish red, 1–1.2 cm. long, with 8 to 20 seeds exserted beyond the

thickened scales. Seeds ovoid, compressed, black, 0.3 to 0.4 cm. long; aril cup-shaped, white, fleshy. Seed cone scales remaining integral; no receptacle formed.

DISTRIBUTION. Endemic to New Zealand (MAP 2). In lowland and montane forests from sea level to 850 meters, rarely to 1000 meters on some mountain peaks, in the northwestern parts of North Island.

REPRESENTATIVE SPECIMENS. **New Zealand.** NORTH ISLAND: Mangonui, Peria, Watts Bush, *H. Carse 2343* (AK); near Whangarei, Mt. Maungatapere, *Carse 641* (AK); Little Barrier Island, *L. Cockayne 6296* (AK); Great Barrier Island, *T. Kirk* (WELT *37769*); Auckland, Birkdale, *Carse 2337* (AK); Coromandel Peninsula, *A. E. Wright 700* (AK); Te Aroha Mts., *W. R. B. Oliver* (WELT *15267*); Rotorua, Mt. Tarawera, *P. Hynes 110361* (AK); Lake Waikare, Aniwaniwa Falls, *D. A. Crawford* (CHR *65355*).

The following specimens are considered to be intermediate forms or hybrids: *WELT 37791*, collected by Thompson from Waitakere Range, New Zealand, is intermediate between *Phyllocladus glaucus* and *P. trichomanoides*; *CHR 186617* and *CHR 186618*, collected by A. P. Druce from Hine River, west of Waikareti, in Ureivera National Park, are between *P. glaucus* and *P. aspleniifolius* var. *alpinus*. Further examination is needed.

3. **Phyllocladus hypophyllus** Hooker f. Ic. Pl. n.s. **5**: *t. 889*. 1852; Carrière, Traité Gén. Conif. ed. 2. 706. 1867; Parlatore in DC. Prodr. **16**(2): 499. 1868; Stapf in Trans. Linn. Soc. Bot. **4**: 249. 1894; Pilger in Engler, Pflanzenr. **4**(5): 99. 1903; Merrill, Enum. Philip. Fl. Pl. 1: 5. 1925; H. Keng in Gard. Bull. Sing. **20**: 123. *fig.* 1963; de Laubenfels in Jour. Arnold Arb. **50**: 278. 1969. TYPE: Borneo. Mt. Kinabalu, alt. 8000 feet and upwards, *H. Low*.

Phyllocladus hypophyllus Hooker f. var. *protracta* Warb. Monsunia **1**: 278. 1900. TYPE: Mindanao, *Warburg 14722*.

Phyllocladus protractus (Warb.) Pilger in Engler, Pflanzenr. **4**(5): 99. 1903.

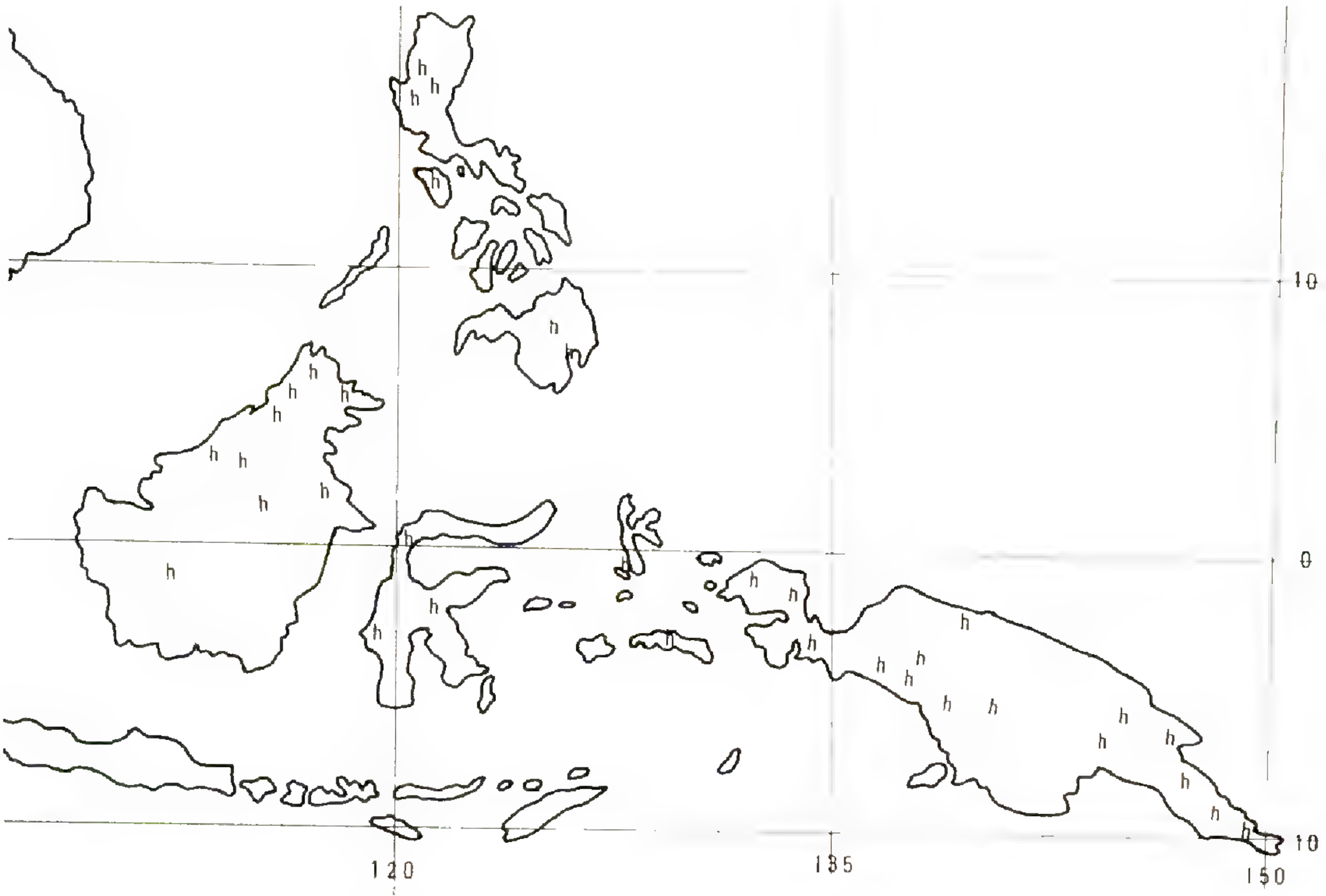
Phyllocladus major Pilger in Bot. Jahrb. **54**: 211. 1916. TYPE: New Guinea, *Ledermann 9872*.

Small or large tree, up to 30 m. or more high. Bark reddish brown to dark brown, flaking, with hard, rough granules, breaking off in large scales. Juvenile leaves on seedlings linear, 0.5–0.8 cm. long. Scale leaves on the short branchlets of adult plant awl shaped, 0.2–0.3 cm. long. Phylloclades on seedlings spathulate to rhomboid, 2–8 cm. long, the apex acute or caudate, the base narrowly attenuate, the margin irregularly serrate, lacerate, or pinnatifid; phylloclades on adult plants pinnately compound, 10–15 cm. long, usually consisting of 5 to 10 segments, the segments oblanceolate, obovate to rhomboid, 1.5–4 cm. (–10 cm. in saplings) long, the upper surface dark green, the lower often glaucous. Plants usually dioecious. Pollen strobili often 2 or 3, sometimes to 15, in clusters on the tip of a short branchlet, sometimes mixed with sterile (but reduced) phylloclades or phylloclades bearing reduced ovulate strobili, yellowish brown, cylin-

drical, 1.2–1.5 cm. long, stalked. Ovulate strobili purplish, solitary or rarely 2 (or 3) together situated in the notch of a bilobed simple phylloclade, or in the notches of the bilobed segments of a compound phylloclade, sometimes these segments becoming columnar or obsolete; each ovulate strobilus ovoid or ellipsoid, consisting of about 15 coalescent scales of which only 2 or 3 are fertile, each bearing a simple, erect ovule. Seeds ovoid, chestnut brown, 5–8 mm. long, flattened, the aril whitish; receptacle yellowish brown, fleshy.

DISTRIBUTION. Endemic to Malesia (MAP 3), from Luzon and Borneo, through the Celebes and Moluccas, to New Guinea. Scattered in montane rain and subalpine forests, on ridges and summits, from 1500 to 3000 meters, and occasionally also from 900 to 4000 meters in some restricted areas.

REPRESENTATIVE SPECIMENS. **Philippines.** LUZON: Mt. Benguet, Panai, *E. D. Merrill 4753* (L); Benguet, Mt. Singakalsa, *M. D. Sulit, PNH 7669* (L). MINDANAO: Bukidnon, Mt. Katanglad, *Sulit, PNH 10052* (L); Davao, Mt. Apo, *R. Robbins s.n.* (L). **Borneo.** SARAWAK: Baram, Mt. Mulu, *J. A. R. Anderson 4544* (L); Melinau, Mt. Api, *P. Chai, S 30366* (L); Mawas, Marigan Range, *E. F. Brunig, S 9984* (L). BRUNEI: Mt. Ulak, *P. Ashton, BRUN 1033* (L). SABAH: Mt. Kinabalu, *J. & M. S. Clemens 29743* (L); *Chew, Corner, & Stainton, RSNB 710* (L); Kudat, Trusmandi, *G. Mikil, SAN 31784* (L). KALIMANTAN: Mt. Semedum, *H. Hallier 697* (L); Banan, Bengkajang, *bb 24777* (L). **Celebes:** Mt. Loemoet, Menado, *P. J. Eyma 3621* (L); Enrekang, Sawito, collector unknown, *bb 20782* (L); Labu, Malili, *A. Burhi, bb 24089* (L). **Moluccas:** Batjan, *de Haan, bb 23236* (L); Obi, *de Haan, bb 23812* (L); Ceram, Mt. Sofia, *E. Stresemann*



MAP 3. Distribution of *Phyllocladus hypophyllus* in Malesia.

133 (L). **Irian Jaya:** Vogelkop Peninsula, Nettoti Range, *van Royen & Sleumer 7403* (L); Kebar Valley, Neetjapaki Mts., *C. Kalkman, BW 6373* (L); Wissel Lake, *Eyma 4954* (L); Lake Habbema, *L. J. Brass 10528* (L); Mt. Antares, Star Mts., *Kalkman 4539* (L). **Papua New Guinea.** W. HIGHLANDS: Mt. Hagen, *Hoogland & Pullen 5871* (L), Lake Inim, *J. R. Flenley, ANU 2177* (L). MOROBE: Mannasat, Cromwell Mts., *R. D. Hoogland 9482* (CANB, L); Mt. Kaindi, *Brass 29692* (CANB, L). S. HIGHLANDS: Mt. Giluwe, *R. Schodde 2014* (CANB, L). CENTRAL: Murray Pass to Woitape, *Forman & Wardle, NGF 45587* (L).

4. **Phyllocladus trichomanoides** D. Don in Lambert, Descr. Genus *Pinus*. ed. 3. 2: 159. 1832. A. Cunningham in Ann. Nat. Hist. 1: 211. 1838; Hooker, Ic. Pl. n.s. 2: *tt. 549–551*. 1843; Endlicher, Synop. Conif. 235. 1847; Hooker f. Fl. Novae-Zeland. 1: 235. 1853; Carrière, Traité Gén. Conif. ed. 2. 705: 1867; Parlatore in DC. Prodr. 16(2): 498. excl. vars. 1868; Kirk in Trans. New Zealand Inst. 10: 381. 1878, Forest Fl. New Zealand, 9. *tt. 6, 7*. 1889; Pilger in Engler, Pflanzenr. 4(5): 97. 1903; Cheeseman, Man. New Zealand Fl. 658. 1906, ed. 2, 119. 1925, Illustr. New Zealand Fl. 2: *pl. 190*. 1914; Allan, Fl. New Zealand 1: 113. 1961. LECTOTYPE: New Zealand. North Island, Wangaroa, *A. Cunningham* (K).

Medium-sized to large tree, 20–23 m. tall. Bark smooth and thick, greenish to dark gray or blackish. Juvenile leaves linear, acute, 0.8–1 cm. long. Scale leaves at the base of young shoots subulate, 0.2–0.3 cm. long. Phylloclades on seedlings usually pinnatifid to pinnately compound, 5–7 cm. long, stalked; those on adult plants pinnately compound, 3–8(–12) cm. long, consisting of 6 to 10 (to 12) segments, the segments broadly rhomboid or ovate-flabellate, 1.2–2.5 cm. long, the margin varying from broadly toothed to deeply laciniate. Plants usually dioecious. Pollen strobili 5 to 10 in a terminal cluster, cylindric, 0.8–1 cm. long, stalked, the stalks 0.3–1 cm. long. Ovulate strobili usually borne on one side of the segments of the pinnate phylloclade, these segments often reduced in various degrees, sometimes merely stalklike; each strobilus irregularly ovoid or subglobose, 0.2–0.3 cm. long, usually consisting of 2 or 3 fertile scales, each possessing a single ovule. Seeds dark blue to black, ovoid, compressed, about 0.3 cm. long, solitary, exserted beyond the crenulate cupular aril and the succulent receptacle.

DISTRIBUTION. Endemic to New Zealand (MAP 2). In lowland and montane forests, from sea level to 800 meters, rarely to 1000 meters in restricted areas, on most parts of North Island (from North Cape to Taranaki and Hawke Bay) and on the northern tip of South Island.

REPRESENTATIVE SPECIMENS. **New Zealand.** NORTH ISLAND: North Cape, Kerr Point, *H. D. Gordon 1993* (WELT); Mangonui, Kaitaia, Oinu, *H. B. Matthews 2328* (AK); Bay of Islands, Russell State Forest, *A. E. Orchard 3794* (AK); Whangarei, Mangakahia Valley, Twin Bridges, *R. Cooper 120085* (AK); Little Barrier Island, *E. M. Smith 109127* (AK); Great Barrier Island, *Cooper* (CHR *206941*); Anawhata Valley, *L. B. Moore & L. M. Cranwell 91345* (AK); Waite-

mata, Waitakere Range, *Orchard 3372* (AK); Manukau, Hunua, *N. J. Pickett 22156* (AK); Coromandel, Whitianga, *A. E. Wright 666* (AK); Pakirarahi, Thames, *J. Adams 14276* (AK); Tauranga, McLaren's Falls, *W. I. Simpson* (CHR *117400*); Gisborne, Motu River, *E. M. Chapman* (CHR *258563*); near New Plymouth, Barratt Lagoon, *A. N. Druce s.n.* (CHR *274998*). SOUTH ISLAND: Marlborough, Okiwi Bay, *H. Talbot* (CHR *270096*); near Nelson, Mai Tai Valley, *P. Wardle* (CHR *179034*); S. E. of Cape Farewell, Puponga, *Druce* (CHR *273456*).

ECONOMIC USES

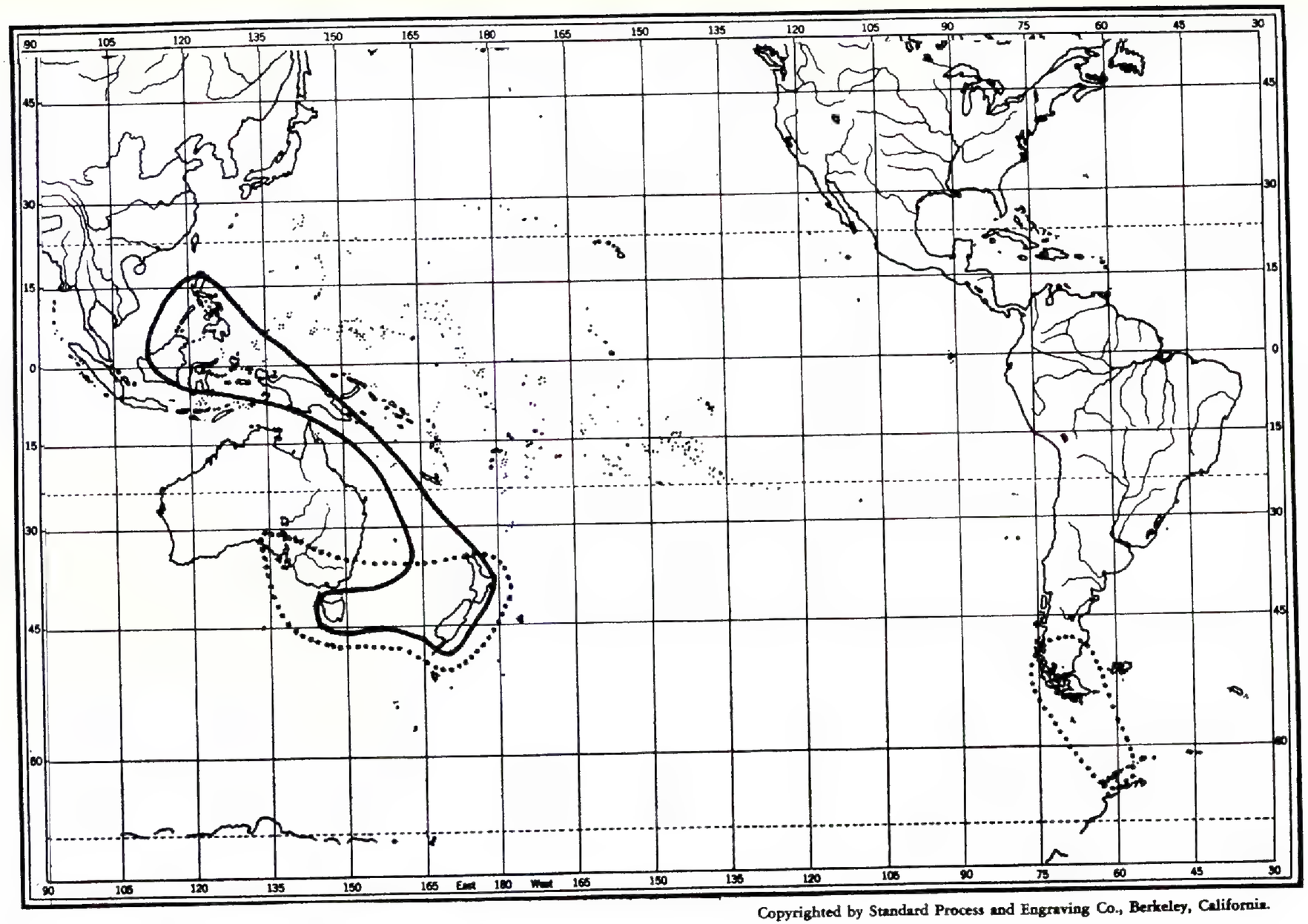
There is not enough timber from any of the four species of celery pine to be of commercial importance. Nevertheless, the wood is white and even grained, and shrinks very little on drying. It is valuable for flooring, boat decks, railway sleepers, mine props and piles, and occasionally for local building purposes and agricultural implements. The bark contains a high percentage (20 to 25%) of tannin, and once was considered to be of great value in tanning. According to Kirk (1889), the bark of two New Zealand species (*Phyllocladus glaucus* and *P. trichomanoides*) also yields a red dye which was formerly used by the Maoris for dyeing their cloaks.

PALEOGEOGRAPHIC DISTRIBUTION

Although *Phyllocladus* is now limited to Tasmania, New Zealand, and eastern Malesia, fossil records reveal its much wider distribution in geologic time. After enumerating and evaluating the paleobotanical data, Couper (1960) reached the following conclusions. (1) Macrofossils identified on the basis of cuticular structure and cladode morphology as *Phyllocladus* are recorded from the Oligocene of continental Australia and the Oligocene, late Tertiary, and Quaternary of New Zealand. (2) Microfossils (pollen grains) are found sporadically in Tertiary sediments in Australia, Tasmania, and New Zealand (MAP 4). In New Zealand they occur from the Oligocene onward, but in Australia they are found mainly in the Oligocene. They are also found in the lower Tertiary of Seymour Island in western Antarctica. (3) No fossils of *Phyllocladus* are known from the Cretaceous or Tertiary of northern South America, New Guinea, Borneo, or India. A phyllocladean affinity has been suggested for some fossil woods from southern South America, but these identifications are inconclusive.

Recent pollen studies by Dodson (1974a, 1974b) indicate that *Phyllocladus* grew in western Victoria and southeastern South Australia during the Quaternary and became extinct only a few thousand years ago. Also according to the same author (pers. comm.), *P. asplenii folius* var. *asplenii folius* was formerly present on Flinders Island in Bass Strait (between mainland Australia and Tasmania). It disappeared from the island at the beginning of this century as a result of an influx of settlers.

The absence of fossils in the tropics and in the Northern Hemisphere deserves special attention. It supports the view that the present extension



MAP 4. Distribution of *Phyllocladus*, present (solid line) and paleogeographic (dotted lines). (Paleobotanical data based on Couper, 1960.)

of *Phyllocladus* into eastern Malesia was a relatively recent development (Hair, 1963; de Laubenfels, 1969).

Among the fifty or so genera of extant conifers, about thirty of them are confined to the Northern and fourteen (including *Phyllocladus*) to the Southern Hemisphere. Li (1953) has summarized the present range of conifers and emphasized the clear differentiation into northern and southern groups. This separation, according to Li, has been shown by paleobotanical records to have existed since the Paleozoic. Nearly all of the considerable number of monotypic or oligotypic genera (including *Phyllocladus*) show restricted or disjunct ranges, grow best in a damp mesophytic habitat, and are practically all confined to lands bordering the Pacific Basin. This is considered by some botanists (including Li) to support the continental drift theory as modified by du Toit, who believed in two ancient land masses, Gondwana and Laurasia, separated by the Tethys Sea. Krassilov (1974), however, feels that the history of conifers has little bearing on the problem of continental drift and suggests that the southern and northern conifers have been more effectively separated by equatorial climatic conditions than by water barriers.

ACKNOWLEDGMENTS

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WOOD ANATOMY AND PHYLOGENY OF PAEONIA SECTION MOUTAN

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THE GENUS *Paeonia* consists of thirty-three species of herbaceous and woody plants. In his classic work on the taxonomy of *Paeonia*, Stern (1946) separated the genus into three sections: MOUTAN, PAEONIA, and ONAEPIA. The section MOUTAN contains four species of shrubs native to western China. The section PAEONIA has twenty-seven species of perennial herbs and occurs from Spain and North Africa through temperate Asia into Japan. The section ONAEPIA, also consisting of perennial herbs, contains two species native to western North America.

De Candolle (1824) placed *Paeonia* within the family Ranunculaceae. Bartling (1830), however, suggested that the genus belonged in a unigeneric family, Paeoniaceae, near the Magnoliaceae. Since then, the phylogenetic position of *Paeonia* has been the subject of considerable debate. Bartling's position has been supported by superficial studies of the wood anatomy (Worsdell, 1908; Kumazawa, 1935). Subsequent investigations of the cytology and floral anatomy, however, have indicated that a more natural position would be in the Dilleniales, near the Dilleniaceae or the Crossosomataceae (Corner, 1946; Lemesle, 1955; Eames, 1961).

Many authors have agreed on the need for more detailed studies on all aspects of this genus. In particular, there has been little study of the secondary wood anatomy. Previous anatomical studies have been concerned only with the amphicribral condition of the vascular bundles (Worsdell, 1908), or with the occurrence of secondary ray tissue and the presence of scalariform perforation plates in the vessels (Kumazawa, 1935).

The genus *Paeonia* is noteworthy in possessing a combination of both advanced and primitive characters. The most important of these combinations is the occurrence of both woody (primitive) and herbaceous (advanced) species. Also, the Paeoniaceae is the only family with herbaceous members (advanced) that possesses scalariform (primitive) vessel perforations (Eames, 1961). The gross morphology of the genus is predominantly primitive; however, a great number of advanced characters may be observed in the wood anatomy. Of special interest is the section MOUTAN, in which the ancestral woody habit has been retained. In addition, this section occurs in a region (western China) noted for its many relict taxa of great age.

MATERIALS AND METHODS

The secondary xylem of 59 samples of the four shrubby species of *Paeonia* section MOUTAN has been examined. Species of the section MOUTAN are distinguished from the other sections of the genus by their peren-

nial, woody stems and by thin petals which are much longer than the sepals.

The section is divided into two subsections (Stern, 1946):

I. Subsection VAGINATAE

1. *Paeonia suffruticosa* Andrews. Samples investigated: twenty-six. Native to the mountains of central China; Kansu, Szechwan, and Shansi provinces; elevation 2130–4270 meters (7,000–14,000 feet).

II. Subsection DELAVAYANAE

2. *Paeonia delavayi* Franchet. Samples investigated: ten. Native to the Likiang Ranges of Yunnan and southwest Szechwan provinces; elevation 3050–3660 meters (10,000–12,000 feet).
3. *Paeonia lutea* Delavay ex Franchet. Samples investigated: twelve. Native to the Tali Range, from northern Yunnan Province northwest into southeastern Tibet; elevation 2740–3660 meters (9,000–12,000 feet).
4. *Paeonia potaninii* Komarov. Samples investigated: seven. Native to the northern border of Yunnan north to western Szechwan Province, elevation 2740–3050 meters (9,000–10,000 feet).

In addition to the samples listed above, four hybrids were investigated: three of *Paeonia delavayi* × *lutea* and one of *P. lutea* × *potaninii*. All samples cited in this paper are identified by the senior author's numbers. Herbarium specimens, which have accompanied some of the wood samples, have been deposited in the herbarium of the University of California, Santa Barbara, California.

Five slides for microscopic examination were prepared from each sample, according to standard methods (Wetmore, 1932). Sections were softened in 48 percent hydrofluoric acid, embedded in celloidin, and cut on a sliding microtome at 15 μm. Sections were stained in Heidenhain's iron alum haematoxylin and safranin. A complete collection of slides is filed with the herbarium sheets.

The terminology used in the anatomical descriptions complies with that approved by the Committee on Nomenclature, International Association of Wood Anatomists (1933, 1964). The choice of diagnostic characters was made largely from the lists prepared by Record and Chattaway (1939) and Tippo (1941). The most frequent range category in each case was arbitrarily determined. All measurements were taken at random. The classification of wood parenchyma distribution utilized here is a synthesis of the one presented by Metcalfe and Chalk (1950) as amended by the International Association of Wood Anatomists (1951).

ANATOMY OF THE SECONDARY XYLEM

An outline of the measurements recorded for the secondary xylem is presented in TABLE 1.

GROWTH RINGS. Growth rings are always present (FIGURE 23), although

TABLE 1. **Secondary xylem of Paeonia.**

CHARACTER	RANGE	MOST FREQUENT RANGE	MEAN
I. **Imperforate elements (Tracheids, fiber-tracheids)**			
a. Length	160–1224 μm. (short–medium)	33–640 μm. (short)	541 μm. (short)
b. Wall thickness	very thin–thick	thin–thick	
c. Pit-pair horizontal diameters	2–8 μm.	3–5 μm.	4.1 μm.
II. **Vessels**			
a. Length	97–1191 μm. (short–medium)	250–500 μm. (short–medium)	380 μm. (medium)
b. Distribution	11–58/mm.^{2}	20–40/mm.^{2}	31/mm.^{2}
c. Transectional diameters	16–88 μm. (extremely small–moderately small)	28–44 μm. (very small)	36.4 μm. (very small)
d. Number of bars in scalariform perforation plates	1–7 (few–intermediate)	1–3 (few)	
e. Width between bars	6–20 μm. (narrow–wide)	8–12 μm. (wide)	
f. End wall angle from the vertical	4–45°	15–30° (very oblique)	
g. Intervascular pit diameters	2–10 μm. (minute–large)	5–7 μm. (small)	6 μm. (small)
III. **Vascular rays**			
a. Tangential frequency	3–16/mm.	6–10/mm.	
b. Width of multiseriate rays	20–124 μm. (2–8 cells) (very fine–broad)	28–56 μm. (2 or 3 cells) (moderately fine)	
c. Width of uniseriate rays	28–37 μm. (moderately fine)		
d. Height of uniseriate rays	128–2430 μm. (1–75 cells) (extremely low–rather low)		570 μm. (very low)
e. Height of multiseriate rays	160–3000 μm. (extremely low–rather low)		620 μm. (very low)

they are occasionally poorly defined. The annual increment varies from relatively narrow to wide.

IMPERFORATE ELEMENTS. The imperforate elements are tracheids and fiber-tracheids. No libriform wood fibers or gelatinous or septate fibers were observed. The walls of the imperforate elements vary from very thin to thick, but are most frequently within the limits of thin to thick (FIGURE 24).

The pit-pairs are bordered and generally circular. The inner apertures of all pits are elongated, and those of the pit-pairs are crossed. The elongated inner apertures do not ordinarily extend beyond the outline of the borders (FIGURES 25, 31).

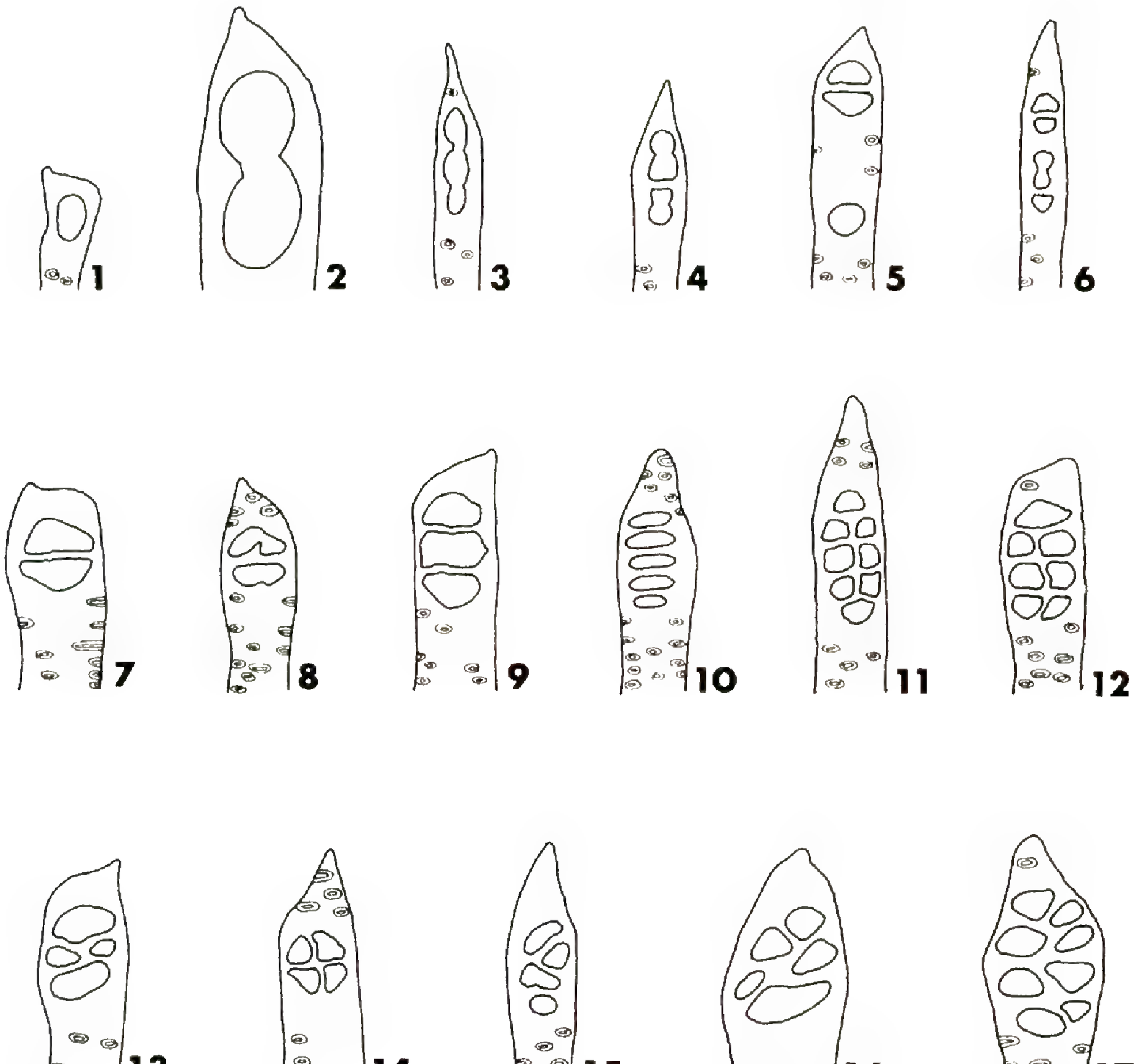
One hundred length measurements of the imperforate cells of each of the 59 samples were taken at random. The lengths of the elements vary from 160 (short) to 1224 μm. (medium sized). The most frequent range is from 33 to 640 μm. (short), and the mean for the genus is 541 $\pm$ 7.04 μm. (short), with a standard deviation of 89.7 $\pm$ 1.16 μm. The proportion of elements with spiral thickenings is quite variable from sample to sample. In some samples, most of the elements have spiral thickenings; in others, this condition is rare or absent. Occasionally, the thickening is a double one, with one coil pitched in one direction and the other one in the opposite direction.

VESSELS. The number of vessels per square millimeter in transverse aspect was calculated from 10 microscopic fields of each sample. Vessel distribution is predominantly of solitary and chain arrangements, but multiples also occur frequently (FIGURE 23). Pore clusters occur occasionally or rarely in 36 of the samples.

Paeonia is usually distinctly ring porous (FIGURE 23), although some rings are indistinct or are only semi-ring porous. The early wood characteristically has larger and more frequent pores than are found in the late wood. The late wood has small pores which are usually fairly evenly distributed. In all species, the vessels are angular in cross section (FIGURES 23, 24). Exceptions were observed in scattered vessels in a few samples of *P. lutea*, where some of the larger vessels were circular or nearly so.

Perforation plates in the end walls of the vessel elements are most commonly of the scalariform type, but other multiperforate forms, as well as simple perforation plates, also occur (FIGURE 31). The number of bars in typical scalariform perforation plates varies from 1 to 7 (few to intermediate) (FIGURES 7–10), and varies most frequently from 1 to 3 (few). The widths of the openings among the bars vary from 6 (narrow) to 20 μm. No borders occur around the perforations.

Of a random count of 2950 perforation plates, 3.7 percent were found to be simple (FIGURES 1–3). The simple perforation plates usually occur in vessels with relatively narrow diameters, and are of three main types. The first type (FIGURE 1) has typically round openings which are most often encountered in the more advanced dicotyledons ("simple perforations" *sensu* Esau, 1965). These perforations occur in vessels with end



FIGURES 1–22. Perforation plates as seen in radial section: 1–4, 6–8, 10–15, 17–20, *Paeonia suffruticosa*; 5, 9, 21, *P. delavayi* × *lutea*; 16, *P. potaninii*; 22, *P. lutea*.

walls most closely approaching the horizontal. The second type of simple perforation is vertically elongate (FIGURE 3). The last type appears similar to a scalariform perforation with the cross bar partially unformed (FIGURES 2, 31). In rare instances, a vessel end wall appears to have two distinct perforation groups, of which one might be simple and the other multiple (FIGURE 5). This latter type might be considered a single scalariform perforation plate, however.

With the exception of the herbaceous Paeoniaceae, scalariform perforation plates in dicotyledons are found exclusively in woody taxa (Eames, 1961). Scalariform vessels have been observed by the writers in *Paeonia californica*, a perennial herb with fleshy roots. The most common pattern in *Paeonia* section MOUTAN could be classified as "typically scalariform" (FIGURES 9, 10); in this form the horizontal bars are arranged in a ladder-like series along the flattened, oblique end wall. This corresponds to the form occurring most frequently in dicotyledonous vessel perforation plates ("scalariform" *sensu* Esau, 1965).

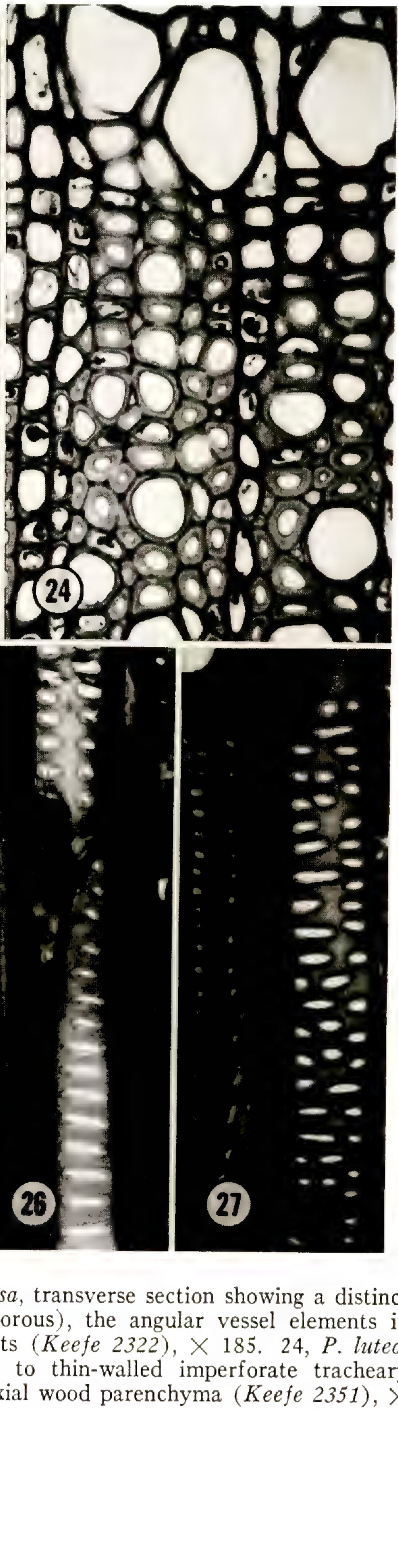
Ten percent of the perforation plates examined were atypical multiperforate forms. These occur in four basic types. The first, and most common, type includes typically scalariform bars with the addition of vertical bars or bar-fragments (FIGURES 8, 11–14). We have named this type modified scalariform. The second type has some plates including irregularly reticulated perforation patterns in oval to circular (FIGURES 15, 18–20), scattered (FIGURE 21), or elongate (FIGURE 22) configurations. In the third type the plates approach foraminate configurations (Gray & de Zeeuw, 1974) (FIGURES 16, 17). The fourth type includes forms transitional between scalariform and simple perforation plates (FIGURES 2–6). Both the first and second types would be considered irregular reticulate plates according to Gray and de Zeeuw (1974).

A similar and distinctive perforation pattern tends to appear in successive end walls, *ad seriatim*, of several members (five to ten) of a single vessel. Distinctive patterns were not observed to be repeated in radially successive vessel members; that is, in derivatives of the same cambial initial. This indicates that a particular perforation pattern may be expressed in a vessel as a unit, rather than in the successive derivatives of a single cambial initial.

The end walls of the vessel elements in tangential aspect are generally quite oblique, ranging from 4 to 45° off the vertical, but vary most frequently from 15 to 30° off the vertical (very oblique) (FIGURES 25, 26).

The intervascular pitting of the vessels varies from transitional to alternate (FIGURES 25–27). Often there is a single staggered row of pit-pairs in the vessel wall (FIGURES 25, 30). The scalariform arrangement was observed in two samples of *P. suffruticosa*, although rarely so even in these cases (FIGURE 26). The size of the intervascular pit-pairs varies from 2 (minute) to 10 μm. (large), but ranges most frequently from 5 to 7 μm. (small), with a mean of 6 μm. Twenty pit-pairs from each of the samples were measured. The intervascular pit-pairs are predominantly circular in outline, but are occasionally elongate, oval, or scalariform. Generally, the pit-pairs have elongate and crossed apertures which in face view do not extend beyond the outlines of the pit borders.

VESSEL–RAY PITTING. The pitting between the vessel elements and the vascular ray cells is variable. Alternate and opposite pitting are the most common, but the transitional arrangement was found frequently in most samples (FIGURE 28). The vessel–ray pits are without borders.



FIGURES 23–27. 23, *Paeonia suffruticosa*, transverse section showing a distinct growth ring boundary (distinctly ring-porous), the angular vessel elements in solitary, chain, and multiple arrangements (*Keefe 2322*), × 185. 24, *P. lutea*, transverse section demonstrating thick- to thin-walled imperforate tracheary elements, a growth ring boundary, and axial wood parenchyma (*Keefe 2351*), ×

VESSEL LENGTH. One hundred length measurements of vessel elements were taken at random from macerated wood of each of the 59 samples. The length of the elements from the tip of one "tail" to the other varies from 97 (short) to 1190 μm. (medium). The most frequent range is from 250 to 500 μm. (short to medium), and the mean for the genus is 380 $\pm$ 4.95 μm. (medium) with a standard deviation of 89.7 $\pm$ 1.16 μm. The vessel elements are often storied (FIGURE 28). Spiral thickenings occur frequently in the vessel elements, and, as in the imperforate elements, they are often double. These occur most often in smaller vessels.

VASCULAR RAYS. The frequency of rays occurring horizontally across a tangential section is from 3 to 16 per mm., and more commonly from 6 to 10 per mm. The vascular rays are both uniseriate and multiseriate. No compound or aggregate rays occur. The ray type is not constant for the section MOUTAN, or for a particular species. The rays, furthermore, do not closely agree with the classical patterns as set down by Kribs (1935). The rays are often heterocellular, but the vertically elongate cells occur randomly throughout a particular ray, rather than exclusively in the wings or distal portions of the ray (FIGURE 30). The classical pattern with elongate cells only at the distal portion of a ray was not observed in any of the samples.

Three basic types of rays were observed. The most common was a modified Heterogeneous Type II (all names of ray types taken from Kribs, 1935). These consist of 40 to 99 percent uniseriate rays, which were in the low or extremely low class in height (FIGURE 30). Generally speaking, the samples which possess a greater percentage of uniseriates tend to have the higher uniseriate rays. The multiseriate rays are most commonly bi- or triseriate. Again, the samples with the higher percentage of uniseriate rays tend to have a greater proportion of biseriate rays than of wider ones.

One sample of *Paeonia suffruticosa* (*Keefe 1301*) has Homogeneous Type I rays. In this sample the uniseriate rays comprise 20 to 30 percent of the total number of rays. The multiseriate rays are almost entirely biseriate with very long wings. The height is in the extremely low class. Although these rays are fairly homocellular, the individual ray cells as seen in face view on tangential sections are intermediate between the traditionally defined round and rectangular-shaped cells.

Three samples, two of *Paeonia suffruticosa* (*Keefe 1051, 1504*) and one of *P. potaninii* (*Keefe 1268*), would agree with Kribs's classification of

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280. 25, *P. suffruticosa*, tangential section illustrating imperforate tracheary elements with circular-bordered pit-pairs and crossed apertures (arrow), vessel elements having oblique end walls and scalariform perforation plates, uniseriate vascular rays, spiral thickenings in imperforate elements, and fusiform axial wood parenchyma (*Keefe 2332*), $\times$ 360. 26, *P. delavayi*, tangential section showing vessel element with scalariform intervascular pitting, and portion of vessel element with opposite to alternate intervascular pitting (*Keefe 2359*), $\times$ 340. 27, *P. delavayi*, tangential section showing vessel element with transitional intervascular pitting (*Keefe 2359*), $\times$ 340.

FIGURES 28–31. *28*, *Paeonia lutea*, radial section showing storied vessel elements and vascular rays with square and upright cells (*Keefe 2351*), × 60. *29*, *P. potaninii* forma *alba*, tangential section showing Homogeneous Type II vascular rays, with infrequent uniseriate and nearly homocellular multiseriate vascular rays, and 3-celled strand axial wood parenchyma (arrow) (*Keefe 1268*), ×

Homogeneous Type II rays. These samples have uncommon uniseriate rays (10 to 20 percent of the total number of rays), and frequent multiseriate rays which are usually wingless (FIGURE 29). The rays are homocellular, being composed entirely of angular to nearly rounded cells as seen in tangential section.

For the section MOUTAN as a whole, the widths of the multiseriate rays vary from 20 to 124 μm. (very fine to broad) or from 2 to 8 cells, as measured horizontally in tangential sections. The majority of multiseriate rays vary within the range of 28 to 56 μm. (moderately fine) or 2 or 3 cells wide, with the exception of the three samples with Homogeneous Type II rays. The uniseriate rays most frequently range from 28 to 37 μm. in width (moderately fine).

Ray height for the genus has a mean of 620 μm. (very low) for the multiseriate rays, with a range of 160 to 3000 μm. (extremely low to rather low). The mean height for the uniseriate rays is 570 μm. (very low), and the range is 128 to 2430 μm. (extremely low to rather low). In number of cells, the uniseriate rays vary commonly from 1 or 2 cells to 75 cells high.

AXIAL WOOD PARENCHYMA. Both strand and fusiform types of axial wood parenchyma occur in all four woody species of *Paeonia*. The most common type is strand parenchyma, with each strand consisting of two cells (FIGURE 30, arrow). Strands with three cells (FIGURE 29, arrow) or fusiform cells (FIGURE 31, arrow) occur less commonly. The axial wood parenchyma is apotracheal and sparse, and occurs in a scattered diffuse pattern among the imperforate elements. In both shape and wall thickness, the axial wood parenchyma is often very similar to the imperforate elements.

DISCUSSION

TAXONOMIC HISTORY. The relationship of the genus *Paeonia* has long been problematic. The genus has been placed in the families Ranunculaceae, Berberidaceae, and Paeoniaceae (and included in the orders Ranales, Paeoniales, Dilleniales, Theales, and Guttiferales) by various authors (TABLE 2).

COMPARATIVE ANATOMY OF THE SECONDARY XYLEM. The following characters of the secondary xylem of *Paeonia* are strictly primitive: (1) presence of tracheids and fiber-tracheids, but absence of libriform wood fibers (Bailey & Tupper, 1918; Bailey, 1936, 1953; Reinders, 1935); (2) absence of septate imperforate elements (Tippo, 1938; Metcalfe & Chalk,

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400. 30, *P. suffruticosa*, tangential section showing vessel elements with oblique end walls; essentially Heterogeneous Type II vascular rays with heterocellular uniseriate and multiseriate rays; multiseriate rays almost entirely two cells wide; and 2-celled strand axial wood parenchyma (arrow) (*Keefe 2332*), × 275. 31, *P. suffruticosa*, radial section showing vessel with typical scalariform perforation plates with 1 and 2 bars, vessel with atypical simple perforation plate, and fusiform axial wood parenchyma (arrow) (*Keefe 817*), × 240.

TABLE 2. **Summary of systematic treatments of the genus Paeonia.**

De Candolle, 1824	Ranunculaceae, near Magnoliaceae
Bartling, 1830	Ranunculaceae
Bentham & Hooker, 1862	Ranunculaceae
Baillon, 1867	Ranunculaceae
Engler & Prantl, 1887, 1915	Ranunculaceae
Hallier, 1905	Berberidaceae
Worsdell, 1908	Paeoniaceae, in Ranales, between Ranunculaceae and Magnoliaceae-Calycanthaceae
Lotsy, 1911	Berberidaceae
Engler & Gilg, 1924	Ranunculaceae
Rendle, 1925	Ranunculaceae, between Lauraceae and Berberidaceae
Heintze, 1927	Paeoniaceae, in Paeoniales, with Ranunculaceae, Berberidaceae, Lardizabalaceae and Menispermaceae
Langlet, 1928	Berberidaceae (including Berberidoideae, Podophylloideae, and Paeonioideae)
Kumazawa, 1935	Paeoniaceae, in Ranales, near Magnoliaceae
Engler & Diels, 1936	Ranunculaceae
Corner, 1946	Paeoniaceae, in Dilleniales, with *Actinidia*
Lawrence, 1951	Ranunculaceae, in Ranales
Lemesle, 1955	Paeoniaceae, in Ranales, between Magnoliaceae and Calycanthaceae-Crossosomataceae
Benson, 1957	Ranunculaceae, between Hernandiaceae and Berberidaceae
Hutchinson, 1959	Paeoniaceae, in Ranales, between Magnoliaceae and Helleboraceae
Eames, 1961	Paeoniaceae, in Dilleniales, near Crossosomataceae
Melchior, 1964	Paeoniaceae, in Guttiferales, near Dilleniaceae
Dickison, 1967	Paeoniaceae, in Dilleniales, near Dilleniaceae
Thorne, 1968, 1974	Paeoniaceae, in Theales, under Dilleniineae
Cronquist, 1968	Paeoniaceae, in Dilleniales, with Dilleniaceae and Crossosomataceae
Takhtajan, 1969	Paeoniaceae, in Paeoniales, between Dilleniales (including Dilleniaceae and Crossosomataceae) and Theales

1950); (3) moderately to very numerous vessels per square millimeter (Frost, 1930a); (4) vessel elements typically angular (Frost, 1930a); (5) vessel elements very small in diameter (Frost, 1930a); (6) vessel elements with scalariform perforation plates (Bailey & Tupper, 1918; Bailey, 1944; (Frost, 1930a, 1930b); (7) vessel elements with oblique end walls (Frost, 1930a; Bailey, 1944); (8) presence of uniseriate and multiseriate rays (Heterogeneous Type IIa) (Kribs, 1935; Barghoorn, 1940, 1941); and (9) axial wood parenchyma scattered, diffuse, and apotracheal (Kribs, 1937; Metcalfe & Chalk, 1950; Carlquist, 1961).

The following characters of the secondary xylem of *Paeonia* are relatively advanced: (1) imperforate elements most frequently with thin to thick walls (intermediate categories) (Bailey, 1936, 1953; Reinders, 1935); (2) imperforate elements and vessels typically with circular-bordered pit-pairs having crossed inner apertures which do not extend beyond the border outlines (Bailey, 1936; Eames & MacDaniels, 1947); (3) length of imperforate elements ranging most frequently from 330 to 640 μm. (short) (Bailey & Tupper, 1918; Chattaway, 1936; Bailey, 1953); (4) vessel distribution commonly of pore chains and multiples in addition to the more primitive solitary condition (Tippo, 1946); (5) ring porosity or semi-ring porosity, ring porosity predominant (Frost, 1930a); (6) number of bars composing the scalariform perforation plates most frequently 1 to 3 (few) (Frost, 1930b); (7) the common presence of wide and (8) non-bordered perforations in the scalariform perforation plates (Frost, 1930b); (9) occasional simple perforation plates (Bailey & Tupper, 1918; Bailey, 1944; Frost, 1930a, 1930b); (10) opposite as well as alternate intervascular pitting (Bailey & Tupper, 1918; Frost, 1931); (11) alternate and opposite as well as transitional pitting between rays and vessels (Bailey & Tupper, 1918; Frost, 1931); (12) length of vessel elements ranging from 250 μm. (short) to 500 μm. (medium) (Bailey & Tupper, 1918; Chattaway, 1936; Bailey, 1953); (13) homogeneous rays (Types I and II) (Kribs, 1935; Barghoorn, 1941); (14) presence of strand axial wood parenchyma, most commonly composed of two cells, rarely accompanied by true fusiform axial parenchyma (Metcalfe & Chalk, 1950); (15) reduced vascular ray structure, with uni- or biseriate rays predominating (Metcalfe & Chalk, 1950); and (16) storied vessel elements (Metcalfe & Chalk, 1950).

The following characters are specialized, but it has not been shown that they represent an advanced condition: (1) occurrence of spiral thickenings in the imperforate elements (Tippo, 1946); (2) presence of spiral thickenings in the vessel elements (Frost, 1931); and (3) presence of atypical multiperforate perforation plates in the vessel elements (Mac-Duffie, 1921; Chalk, 1933; Gottwald & Parameswaran, 1964).

The preceding lists support the hypothesis that the secondary xylem of *Paeonia* cannot be considered primitive. Although several characters are of a primitive nature, a greater number are moderately specialized, and a few are highly specialized. In view of this evidence, one must tentatively

conclude that the family Paeoniaceae has reached a moderate level of specialization.

It is difficult to attach any phyletic importance to the presence of the atypical multiperforate perforation plates. Atypical plates have been reported in many unrelated families. Aldridge (1964) described a definite abnormality of the regular perforation in tomatoes. This is the phenotypic expression of a genetic aberration. Chalk (1933) and Gottwald and Parameswaran (1964) found plates composed of very numerous isodiametric openings which are similar in both size and shape to the bordered pits on the side walls of the vessels. There is no evidence reported of fusion between these perforations within a plate. Multiperforate plates may occur intermittently in a plant and are usually found in taxa with otherwise simple perforation plates. This type undoubtedly has no significance in the evolution of the vessel as a whole, but rather is an anomaly in which the pattern of the intervascular pitting is imposed on the end walls.

The atypical perforation plates found in *Paeonia* represent modifications of scalariform or reticulate plates or are retentions of more primitive perforation plates like those described for other taxa (Thompson, 1923; Dickison, 1967; Gray & de Zeeuw, 1974). Gottwald and Parameswaran (1964) described similar forms as occurring in the Dipterocarpaceae and believed that they were intermediate steps in the evolution of simple perforation plates from scalariform ones.

This is very possibly the case in *Paeonia*, where both scalariform and simple perforation plates exist. In his study on the secondary xylem of the Compositae, Carlquist (1959, 1960) occasionally found multiperforate plates, often in radial series, associated with the normally occurring simple perforation plates. This fact indicates that a single cambial initial tends to produce a series of atypical perforation plate patterns. This situation is different from the condition in *Paeonia*, where similar atypical patterns were found to occur in successive end walls of a single vessel, rather than in radial series.

Atypical multiperforate plates have been reported sporadically, but not infrequently, in scattered families of angiosperms, including both primitive and advanced taxa, as well as in ferns and other lower groups. MacDuffie (1921) states that this condition is particularly prevalent in dicotyledons with herbaceous and climbing habits, but this is not confirmed by a search of other papers treating the subject (Chalk, 1933; Thompson, 1923; Webber, 1936; Bailey & Howard, 1941; Heimsch, 1942; Young, 1955; Carlquist, 1959, 1960, 1961; Eames, 1961; Gottwald & Parameswaran, 1964; Dickison, 1967).

TABLE 3 shows a comparison of the various characters of the secondary xylem of *Paeonia* with those of other taxa with which it has been variously allied in the past. In summary, on the basis of the secondary wood anatomy alone, the woody species of *Paeonia* are similar to, but more advanced than, the Dilleniaceae and Actinidiaceae, and are similar to, but slightly more primitive than, the Calycanthaceae and Annonaceae. Borderline taxa, in which there is a possibility of relationship, but much less than in com-

TABLE 3. **Comparison of secondary xylem of Paeonia and other taxa.**

	Magnoliaceae	Winteraceae	Canellaceae	Annonaceae	Myristicaceae	Calycanthaceae	Ranunculaceae (Clematis) Berberidaceae	Dilleniaceae	Crossosomataceae	Rosaceae	Spiraeoideae	Rosoideae	Maloideae	Prunoideae	Theaceae	Actinidiaceae	Saurauiaceae	Guttiferae
IMPERFORATE ELEMENTS																		
Type	+	P	A	A	A	A	A	A	+	A	±	A	+	+	+	+	+	A	A
Length	P	P	P	P	P	P	+	+	P	O	P	P	P	P	P	P	O	P	P
Spiral thickenings	P	P	P	P	P	+	P	P	P	P	+	+	+	+	+	P	P	P	P
VESSELS																			
Porosity	+		P	+	P	A	A	+	P	A	±	P	+	+	P	+	P	P	P
Pore distribution	P		P	+	P	A	A	P	+	P	P	P	P	P	P	P	P	P	P
Pore diameter	A		P	+	A	+	O	+	+	+	A	A	A	A	A	A	+	A	A
Cross-sectional outline	+		+	A	A	+	O	+	A	+	A	A	A	A	A	A	+	O	+	A
Perforation plates	P		P	A	+	A	A	A	+	A	A	A	A	A	A	P	A	P	A
Number of bars	P		P	O	+	O	O	A	P	O	O	O	O	O	O	P	P	P	P
Intervascular pitting	P		P	+	P	A	A	A	P	A	A	A	A	A	A	P	O	P	A
Ray-vessel pitting	P		P	A	P	A	A	A	P	A	A	A	A	A	A	P	O	P	P
Ray-vessel pits bordered	+		P	+	P	+	+	+	+	+	+	+	+	+	+	P	O	+	+
Length	P		P	+	P	+	+	A	P	O	P	P	P	P	P	P	P	P	P
Spiral thickenings	+		P	+	+	+	+	+	P	P	P	P	+	+	+	+	+	+	P
VASCULAR RAYS																			
Type	P	P	A	A	+	+	P	A	P	P	+	+	+	+	+	P	P	P	P
Widths of multiseriates	A	A	+	A	+	+	A	A	A	A	A	A	A	A	A	+	A	A	A
Sheath cells common	+	A	+	+	+	+	A	A	A	+	+	+	+	+	+	A	+	+	+
AXIAL WOOD PARENCHYMA																			
Type	+	+	+	+	+	O	A	P	+	O	+	+	+	+	+	O	+	O	O
Number of cells in strand	P	P	P	P	P	+	P	P	O	P	O	O	O	O	O	O	P	O	O
Parenchyma distribution	A	A	A	A	A	A	A	P	+	A	A	A	A	A	A	A	+	A	A
Percentage of characters identical to those of Paeonia	33	10	19	50	29	50	33	33	37	25	45	21	26	32	32	26	38	21	11
Percentage of characters of a lower phyletic level than those of Paeonia	52	60	65	15	52	11	11	24	47	31	25	37	26	26	32	58	50	58	52
Percentage of characters of a higher phyletic level than those of Paeonia	15	30	16	35	19	39	56	43	16	44	30	42	48	42	36	16	12	21	37

\+ Family in question has essentially the same secondary xylary feature as found in Paeonia

P Character of the family in question is less specialized than that of Paeonia

A Character in question is more specialized than that of Paeonia

O Knowledge of character is lacking, or phyletic nature not understood

parison to the families noted above, are the families Magnoliaceae and Berberidaceae, the rosaceous subfamilies Maloideae and Prunoideae, and the ranunculaceous genus *Clematis*. About one-third of the secondary xylary characters of these latter taxa lie at a phyletic level similar to those of *Paeonia*.

CORRELATION OF TAXONOMIC AND MORPHOLOGICAL FEATURES WITH XYLEM

CHARACTERS. It is unwise to speculate concerning phyletic relationship solely on the basis of secondary wood anatomy (Bailey, 1951, 1953). Considering that similar structures appear in quite distantly related taxa due to the frequent occurrence of parallel evolution, no single line of evidence should be considered conclusive. Since a taxon which retains primitive secondary wood characters cannot be derived from one which is uniformly advanced, Bailey (1957) has pointed out that the evidence obtained from secondary wood anatomical studies is often more helpful in negations than in positive assertions of close alliance.

Bailey (1951, 1953, 1957) has also stressed that meaningful phylogenies can be constructed only when comprehensive studies, taking into account evidence from all organs and parts of the plant body, have been evaluated. For this reason, TABLE 4 has been prepared to show differences and similarities of features other than those of the secondary wood, between *Paeonia* and each of the taxa with which it has been linked.

As familial taxonomic descriptions are readily available, they are not included here. The principal works used in compiling TABLE 4 are those by Rendle (1925), Gunderson (1950), Lawrence (1951), Hutchinson (1959), and Melchior and Werdermann (1964). The characters chosen for comparison are those for which information is available in these standard works.

The morphological characters of the Paeoniaceae that have been shown to be primitive (Hutchinson, 1959; Eames, 1961; Davis & Heywood, 1963) include: woody and perennial habit (section MOUTAN); spiral arrangement of leaves; bisexual, solitary, and actinomorphic flowers with many free parts, spirally arranged; hypogynous stamens; several free carpels; and follicular fruit. Those characters of *Paeonia* which are commonly considered advanced or specialized include herbaceous habit (sections PAEONIA and ONAEPIA); deciduous and pinnately compound leaves; absence of stipules; fasciculate stamens; and tricolporate pollen. In addition, Camp and Hubbard (1963) found an abundant vascular supply subtending the ovules of *Paeonia lactiflora* (section PAEONIA). From this they suggest that the ovules in *Paeonia* are specialized through reduction from an ancestral type.

It can be seen, therefore, that the Paeoniaceae may be considered to have predominantly primitive characters. The relatively specialized wood anatomy, however, possibly invalidates the placement of the family in the traditional positions near families that have similar primitive morphology, but that possess dissimilar primitive wood anatomy.

TABLE 4. Comparison of morphological-taxonomic character-states.

	Paeoniaceae	Magnoliaceae	Winteraceae	Canellaceae	Annonaceae	Myristicaceae	Calycanthaceae	Ranunculaceae	Clematis	Helleborus	Berberidaceae	Dilleniaceae	Crossosomataceae	Rosaceae	Spiraeoideae	Rosoideae	Maloideae	Prunoideae	Theaceae	Actinidiaceae	Saurauiaceae	Cuttiferae
Habit woody	+	+	+	+	+	+	+	-	+	+	±	+	+	±	±	±	+	+	+	+	+	+
Vines absent	+	+	+	+	-	+	+	+	-	+	+	-	+	+	+	+	+	+	+	-	+	+
Deciduous	+	±	-	-	±	-	±	±	+	-	±	-	-	±	+	±	±	±	-	-	-	-
Stipules absent	+	+	+	+	+	+	+	+	+	+	+	±	-	-	-	-	-	-	+	-	+	+
Leaves alternate	+	+	+	+	+	+	-	±	-	+	+	±	+	+	+	+	+	+	+	+	+	-
Leaves pinnately compound	+	-	-	-	-	-	-	±	±	+	±	±	-	±	-	±	±	-	-	-	-	-
Flowers solitary	+	+	-	-	+	-	+	±	±	-	-	+	+	±	-	±	-	-	+	-	-	+
Flowers bisexual	+	+	+	+	+	-	+	±	-	+	+	±	+	+	±	+	+	+	±	±	±	±
Bracts present	+	-	0	+	+	0	+	+	-	0	+	-	+	+	±	+	+	+	+	0	+	-
Sepals not fugacious	+	+	+	+	+	+	0	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+
Sepals 5	+	-	±	±	-	-	-	±	+	±	+	+	+	+	+	+	+	+	+	+	+	±
Petals 5-10	+	-	-	±	-	-	-	+	-	±	±	+	+	+	+	+	+	+	+	+	+	±
Stamens many	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+
Stamens spiral	+	+	+	+	+	+	-	+	+	+	-	+	-	-	-	-	-	-	+	0	0	0
Stamens hypogynous	+	+	+	+	+	+	-	+	+	+	+	+	+	±	±	±	-	±	+	+	+	+
Stamens fasciculate	+	-	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	+
Stamens centrifugal	+	-	-	0	-	+	0	-	-	-	-	+	0	-	-	-	-	-	+	+	+	0
Anthers opening lengthwise	+	+	+	-	+	+	+	+	+	+	±	+	+	+	+	+	+	+	+	±	-	+
Disc present	+	-	-	-	0	0	-	-	-	-	-	-	+	+	+	+	+	+	-	-	-	-
Nectaries present	+	-	0	-	0	+	-	±	-	+	±	-	0	0	0	0	0	0	-	-	0	-
Stigma sessile	+	-	+	-	-	+	-	-	-	-	±	-	±	-	-	-	-	-	-	-	-	±
Apocarpous	+	+	+	0	±	+	+	+	+	+	-	+	+	±	+	±	-	-	-	-	-	0
Carpels 2-5	+	-	±	+	-	-	-	-	-	+	-	+	+	±	+	-	+	+	+	+	+	±
Ovules several	+	-	±	+	±	-	-	+	-	+	±	±	+	±	±	+	-	-	±	+	+	±
Ovules anatropous	+	+	+	+	+	+	+	+	+	+	+	±	-	±	±	±	±	±	+	+	+	+
Placentation parietal	+	+	±	+	+	+	+	+	+	+	±	+	+	-	-	-	-	-	-	-	-	±
Fruit a follicle	+	±	-	-	-	-	-	±	-	+	-	±	+	±	+	-	-	-	-	-	-	-
Pollination by beetles	+	+	+	+	+	+	+	±	±	0	0	0	0	-	-	-	-	-	-	+	+	0
Pollen 3-colporate	+	-	-	-	-	-	-	-	-	-	-	±	+	+	+	+	+	+	+	+	+	+
Endosperm copious	+	+	+	+	+	+	-	+	+	+	+	+	-	-	-	-	-	-	-	+	+	-
Embryo small	+	+	+	+	+	+	-	+	+	+	+	+	-	+	+	+	+	+	-	+	+	-
Nucellus crassinucleate	+	+	+	+	+	+	-	+	-	+	+	+	0	+	+	+	+	+	-	-	-	-
Integuments 2	+	+	+	+	+	+	+	+	-	+	+	+	+	±	±	±	±	+	+	-	-	+
Aril present	+	+	0	-	+	+	-	-	-	-	±	+	+	-	-	-	-	-	-	-	-	+
Raphides absent	+	+	+	+	+	0	+	+	+	+	+	-	-	+	+	+	+	+	+	-	-	+
Basic chromosome number	5	10	13-19	13	7, 13	7	11	7-9	8	8	6, 14	8, 13	12	7-9	8, 9	7, 8	17	7, 8	15	58-80	?	16
Number of characters identical to those of *Paeonia* in at least some members	35	23	23	23	23	23	15	26	18	24	21	28	21	25	23	23	20	20	21	17	19	20
Percentage of characters identical to those of *Paeonia* in at least some members	100	66	75	73	73	65	47	74	51	71	62	85	68	71	68	68	59	59	60	52	58	63

\+ Characters identical to those of *Paeonia*

\- Characters different from those of *Paeonia*

± Characters identical at least in some members to those of *Paeonia*

0 Character unknown

Members of the family Dilleniaceae possess the highest number of morphological characters similar to those of *Paeonia* (85 percent, TABLE 4). In addition, it is one of the five families most possibly related to *Paeonia* on the basis of the secondary wood anatomy alone. Morphologically, the families are extremely similar, differing, in characters considered, only by the presence in Dilleniaceae of occasional climbing forms, usually simple leaves, a free stigma, a basic chromosome number of $n = 8$ to 13, and the absence of a disc and nectaries. *Paeonia* can be seen to be more specialized than species in the family Dilleniaceae, especially in its deciduous habit and in its secondary wood, which exhibits such specialized features as ring or semi-ring porosity, short imperforate and vessel elements, a reduction in the number of bars in the scalariform perforation plates (from 20 to 130 down to 1 to 3), and a reduced vascular ray structure (TABLE 3).

Takhtajan (1969) considers *Paeonia* the component of an unigeneric family and order, thereby separating it somewhat more from the Dilleniaceae than do the present writers. His separation is based upon the following morphological characters: (1) thick, fleshy carpels, (2) broad stigmas, (3) a lobed and unusually prominent staminal nectariferous disc, (4) a massive outer integument, (5) seed coat characters, and (6) the peculiar embryogeny described by Yakolev and Yoffe (1957), Cave, Arnott, and Cook (1961), and Walters (1962).

Because of the frequency with which *Paeonia* has been placed within the Ranunculaceae, a discussion of the relationship between these two taxa seems appropriate. The similarities between the Paeoniaceae and Ranunculaceae (and often with the "Ranales" in general) include: usually perennial and herbaceous habit; alternate, more or less divided leaves; bisexual flowers with free and spiral or spirocyclic parts; numerous stamens; free and numerous carpels; follicular or achenial fruits; and seeds containing copious, oily endosperm with a small embryo at the apex.

The separation of *Paeonia* from the Ranunculaceae, however, is strongly indicated in TABLE 5, in which the major and fundamental differences between the two taxa are listed.

Of the differences separating *Paeonia* and the Ranunculaceae, several characters of *Paeonia* also separate that genus from the "Ranales" in general (*sensu* Eames, 1961): amphicribral vascular bundles, fasciculate and centrifugal stamens, and several characters of the ovule, pollen, and secondary wood.

The "Ranalian" families that are most similar to the Paeoniaceae on the basis of the secondary wood anatomy (TABLE 2) are the Calycanthaceae and the Annonaceae, with one-half of the total characters used similar to those found in *Paeonia*. The Calycanthaceae, however, are quite dissimilar to *Paeonia* in morphological features (TABLE 4) and are therefore unlikely to be related.

The family Annonaceae is chiefly tropical and seems to be a reduced or specialized taxon closely related to the Magnoliaceae. Characters which show this relationship are the whorled perianth, exstipulate leaves, and ruminate endosperm. In these features, the Annonaceae are most closely

TABLE 5. **Comparison of Paeonia and Ranunculaceae.**

CHARACTER	*Paeonia*	*Ranunculaceae*
1. Habit	Woody and herbaceous perennials	Herbaceous perennials, woody vines (*Clematis*), or rarely shrubs (*Xanthorrhiza*)
2. Vascular bundles	Amphicribral	Frequently amphivasal
3. Perianth delimitation	Gradation gradual from leaves through bracts, sepals, and petals	Perianth sharply delimited from leaves and bracts
4. Receptacle	Somewhat concave	Convex
5. Vascular supply to perianth	Sepals and petals receiving few to several vascular traces	Sepals typically receiving three traces, petals receiving one trace
6. Petal derivation	From bracts	Probably from stamens
7. Sepals	Persistent	Fugacious
8. Stamens	Fasciculate, developing centrifugally	Free, developing centripetally
9. Subgynoecial disc	Present	Absent
10. Ovule development	With outer integument strongly developed and thick; nucellus crushed, embryo sac enclosed by inner integument, hypostase invariably present; antipodal cells ephemeral	Outer integument similar to the inner integument; nucellar epidermis persisting and enclosing the embryo sac, hypostase rarely present; antipodal cells persistent
11. Seed	Aril present	Aril absent
12. Pollen	3-colporate	3-colpate
13. Seed germination	Hypogeal	Epigeal (except in part of *Clematis*)
14. Basic chromosome number	$n = 5$	$n = 7, 8, 9$
15.* Imperforate elements	Xylary fibers and fiber-tracheids	Libriform wood fibers
16.* Vessels	Small and often solitary, with scalariform and simple perforation plates	Large and usually clustered, with simple perforation plates only
17.* Sheath cells	Absent in vascular rays	Common in vascular rays
18.* Axial wood parenchyma	Apotracheal	Paratracheal
19. Phloem	With little or no sclerenchyma	With many fiber and stone cells
20. Accessory cortical bundles	Present	Absent

* Items 15 through 18 present a comparison of the secondary xylem of *Paeonia* with that of *Clematis*. The latter genus provides the only basis for comparison in this respect.

related to the more advanced genera of the Magnoliaceae, such as *Liriodendron*. The Magnoliaceae and Annonaceae resemble one another in so many ways that the two families are doubtless derived from the same ancestral stock, with the Annonaceae being somewhat more advanced. This advancement has brought the Annonaceae within its alliance up to a phylogenetic level similar to that of *Paeonia*. Because of the basic differences between *Paeonia* and the "Ranales", and the probability of close relationship between the Magnoliaceae and the Annonaceae, the similarities of *Paeonia* and the Annonaceae are probably the result of parallel evolution, rather than of close relationship.

According to TABLE 3 (wood anatomy), the Theales, including the Theaceae, Actinidiaceae, and Saurauiaceae, seem to be closely related to the Dilleniales. Morphologically, the family Theaceae represents a direct syncarpous derivative from the more primitive order Dilleniales. The alliance of the Dilleniaceae to the Theaceae (Thorne, 1968, 1974) is supported by anatomical considerations. The greatest agreement between the anatomy of the two families exists between the subfamily Dillenioideae and the tribes Actinandrieae and Ternstroemieae in the Theaceae (Dickison, 1967).

The Guttiferae are most often placed in their own order in close association with the Theales. The Guttiferae (Theales and Dilleniales) are also seen as advanced syncarpous types, with opposite leaves, and free or variously connate stamens. The stamens are often united into specialized bundles (phalanges). Morphologically, the Guttiferae show little relationship to *Paeonia*, and the secondary wood anatomy is completely dissimilar (TABLE 3).

These two orders, the Theales and the Guttiferales, were more likely derived from a dilleniaceous stock in one evolutionary direction. The secondary wood of the Actinidiaceae shows a phylogenetic level similar to that of the secondary wood in *Paeonia*, but this is not necessarily indicative of close relationship. The different direction taken by these taxa may be seen in the development of carpels and stamens that are more united, a lianous habit (in *Actinidia* and several genera of the Dilleniaceae), and opposite leaves (Guttiferae).

Members of the family Rosaceae are characterized by the usual presence of stipules, a generally pentamerous flower, a hypanthium (in most genera), and the near absence of endosperm in the seed. This family represents a large and eminently successful modification from the "Ranales" by the development of a hypanthium. It has been suggested that the Dilleniales represent the link between the "Ranales" and the Rosales (Porter, 1959). This view, however, is questionable on the basis of specializations found in the Dilleniales which apparently have been retained by other taxa arising from the same ancestral stock, but which are not found in the Rosales (e.g., the centrifugal stamens which are found in the Dilleniales and Theales, but not in the Rosales). Characters found in the Rosaceae which show no similarities to any condition in the Dilleniaceae or in *Paeonia* include the hypanthium, leaves with stipules, free and centripetal

stamens, axile placentation, nearly absent endosperm, and the absence of arillate seeds. In total number of morphological characters, *Paeonia* and the Rosaceae might be considered somewhat similar (TABLE 4), but the important differences already mentioned do not support such a conclusion. Also, treating the four subfamilies separately, as was done in the anatomical treatment, reduces the number of morphological similarities to less than that shown by the family as a whole. Although the Maloideae and Prunoideae exhibit fewer morphological characters similar to those in *Paeonia* than do the other subfamilies, they are anatomically closer to the Paeoniaceae than are the Spiraeoideae or Rosoideae. This is further evidence of the probability that the two taxa are not closely related.

The monogeneric family Crossosomataceae has been included either in the Rosales (Gunderson, 1950; Thorne, 1968) on the basis of the hypanthium, or in the Dilleniales (Hutchinson, 1959; Eames, 1961) on the basis of the free follicular carpels and strongly arillate seeds. Metcalfe and Chalk (1950) and Dickison (1967), however, question the placement of *Crossosoma* within the Dilleniales because of their rather dissimilar anatomy. This view is supported by the lack of similarities between the secondary xylary anatomy of *Paeonia* and that of *Crossosoma* (TABLE 3). In general, the secondary wood of *Crossosoma* contains more highly advanced features than does that of *Paeonia*. Both of these taxa are probably northern derivatives and end-line specializations of larger tropical groups.

CONCLUSIONS

The secondary wood of *Paeonia* shows both primitive and advanced features, with the majority of characters being relatively specialized or advanced. The comparative morphology of the taxa previously held to be related to *Paeonia* clearly indicates that relationship to the Dilleniaceae is very close. The secondary wood anatomy does not negate this conclusion, but further suggests that *Paeonia* is most probably best placed as a valid and distinct unigeneric family within the Dilleniales, somewhat more specialized than the Dilleniaceae. There is a great deal of evidence from morphology, wood anatomy, and cytology to show that *Paeonia* should not be linked with the Ranunculaceae; furthermore, similar evidence nearly as strongly negates close relationship with the other taxa discussed above except for the Theales.

It is noteworthy that the authors' association of *Paeonia* with the Dilleniaceae agrees with the concepts of Corner (1946), Eames (1961), Melchior and Werdermann (1964), Dickison (1967), Thorne (1968, 1974), Cronquist (1968), and Takhtajan (1969). The evidence assembled by the writers, however, does not indicate that the relationship of *Paeonia* with the Crossosomataceae is as significant as is implied by the systems of Eames (1961), Cronquist (1968), and Takhtajan (1969). Closer to our views are those of Corner (1946), Dickison (1967), and Thorne (1968, 1974) that suggest a relationship of *Paeonia*, Dilleniales, and Theales, excluding Crossosomataceae. The proportions of similar anatomical and

morphological-taxonomic characters assembled in TABLES 3 and 4 indicate that *Paeonia* should be included as a distinct family within the Dilleniales. Our assemblage of characters also shows the probability of a close relationship between the Dilleniales (including only the Dilleniaceae and Paeoniaceae) and the Theales.

The Paeoniaceae probably arose from dilleniaceous ancestors in the Indo-Malayan region, the present center of distribution of the Dilleniaceae, and migrated northward into western China. The ancestral types still persist in the higher mountains of western China as the section MOUTAN. The more specialized herbaceous forms have spread west across temperate Eurasia and northeast into western North America.

ACKNOWLEDGMENTS

Grateful thanks are due to Dr. Katherine Esau, for helping to interpret the perforation plate types, and to Mr. Robert Gill for technical assistance.

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A SPECTACULAR BUCHNERA (SCROPHULARIACEAE) FROM COLOMBIA

D. PHILCOX

DURING A STUDY VISIT to the Gray Herbarium and Arnold Arboretum, in preparation for a revision of the extra-African Old World *Buchnera*, the author discovered several specimens of an unidentified plant appearing to represent a species of that genus from South America. The descriptive labels, which gave the flower color variously as scarlet, vermilion, orange-red, or red, cast doubt on its identity. Hitherto, all other species of *Buchnera* have had flower colors in the range from mauve through blue to pinkish lilac or white, but never red. However, following my eventual study of this plant together with the excellent color photographs accompanying *Zarucchi 2143*, I have no hesitation in describing it as new.

Buchnera rubriflora Philcox, sp. nov.

Ab species aliis *Buchnerae* in floribus rubris et capsulis leviter compressis differt.

Annual or perennial herb 20–60 cm. tall. Stem slender, erect, simple or branched from the base, minutely pubescent with adpressed antrorse hairs to subglabrous. Leaves: cauline, 12–30(–45) mm. long, 1–2(–4) mm. wide, opposite to subopposite, narrowly linear, entire, 1-nerved, glabrous to minutely scabrid; basal, 8–22 mm. long, 4–7.5 mm. wide, obovate to obovate-oblong, narrowed into petiole-like base up to 2 mm. long, pinnately nerved, all nerves prominent beneath, with secondary nerves strongly reticulated. Inflorescence slender, lax to compact, up to 8 cm. long; bracts ovate, up to 2.5 mm. long, shortly ciliate, otherwise glabrous; bracteoles linear, shorter than bracts. Calyx erect, to about 4.5 mm. long including teeth 2 mm. long, glabrous except for shortly ciliate teeth, clearly 10-nerved with no intermediate nervation, teeth becoming patent in fruit. Corolla bright red, tube slender, up to 5 mm. long, glabrous, strict to slightly arcuate, densely villous at throat, internally shortly pilose, lobes about 4 mm. long, 3 mm. wide, broadly obovate, shallowly emarginate. Stigma clavate, style persistent in fruit. Capsule to about 3.5 mm. long, compressed-globose, rarely equaling but not exceeding calyx.

HABITAT. Dry, sandy savannas up to 450 meters.

DISTRIBUTION. Known only from Vaupés, Colombia.

REPRESENTATIVE SPECIMENS. **Colombia.** VAUPÉS: Río Kuduyarí, Cerro Yapobodá, ca. 450 m., *Schultes & Cabrera 14211* (A, *holotype*), *Schultes, Baker, & Cabrera 18543* (A); Río Karurú, Mesa de Yambí, Savanna Goo-ran-hoo-dá, *Schultes & Cabrera 19132* (GH), *19141* (GH); Río Kubiyú, Mitú and vicinity, *Zarucchi 2143* (GH, K).

HERBARIUM, ROYAL BOTANIC GARDENS
KEW, RICHMOND, SURREY
ENGLAND

POLLEN OF TROPICAL TREES. I. TILIACEAE

E. Martínez-Hernández, P. Fernández, and S. Lozano

Since the family Tiliaceae is predominantly tropical, and some of its members are important elements of tropical ecosystems, we have chosen to study and describe the pollen of a few of them. We worked with five species of five different genera, representatives of the flora of tropical Mexico, each one described and illustrated in the *Manual para la Identificación de Campo de los Principales Arboles Tropicales de México*, by T. D. Pennington and J. Sarukhán. These species are: *Apeiba tibourbou* Aublet, *Belotia mexicana* (DC.) K. Schum., *Carpodiptera ameliae* Lundell, *Heliocarpus donnell-smithii* Rose, and *Luehea speciosa* Willd.

Our descriptions are accompanied by photographs taken with a Zeiss light microscope and with an AMR scanning electron microscope (SEM).

The specimens studied under the light microscope were obtained from the Herbario Nacional de México (MEXU), while those studied under the SEM were from the collections of the Harvard University Herbaria (A[1] or GH[2]). The specimens from MEXU were acetolyzed (Erdtman, 1952) and mounted with glycerine jelly; those from A or GH were coated with carbon and gold-palladium.

Pollen of most of the genera studied has been described before by various authors: *Apeiba* by Sharma (1969), *Belotia* by Erdtman (1952), *Carpodiptera* by Erdtman (1952) and by Chaudhuri (1965), and *Luehea* by Mohl (1835).

The pollen specimens are deposited in the pollen reference collection of the Paleobotanical Laboratory in the Harvard University Herbaria building and at the Palynological Section of the Museo de Micropaleontología at the Instituto de Geología Universidad Nacional Autónoma de México.

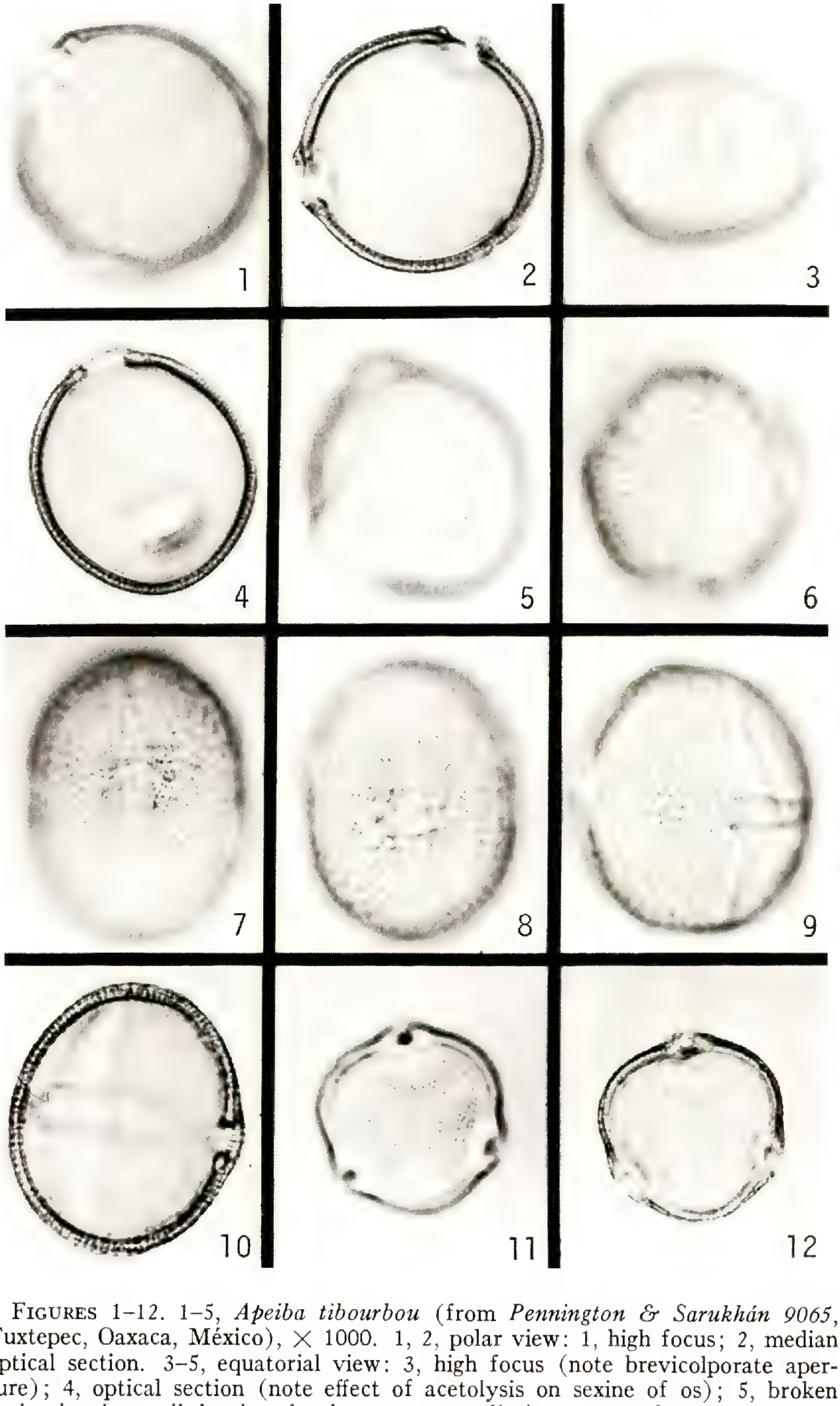
DESCRIPTIONS

Apeiba tibourbou Aublet. Figures 1–5, 25, 32.

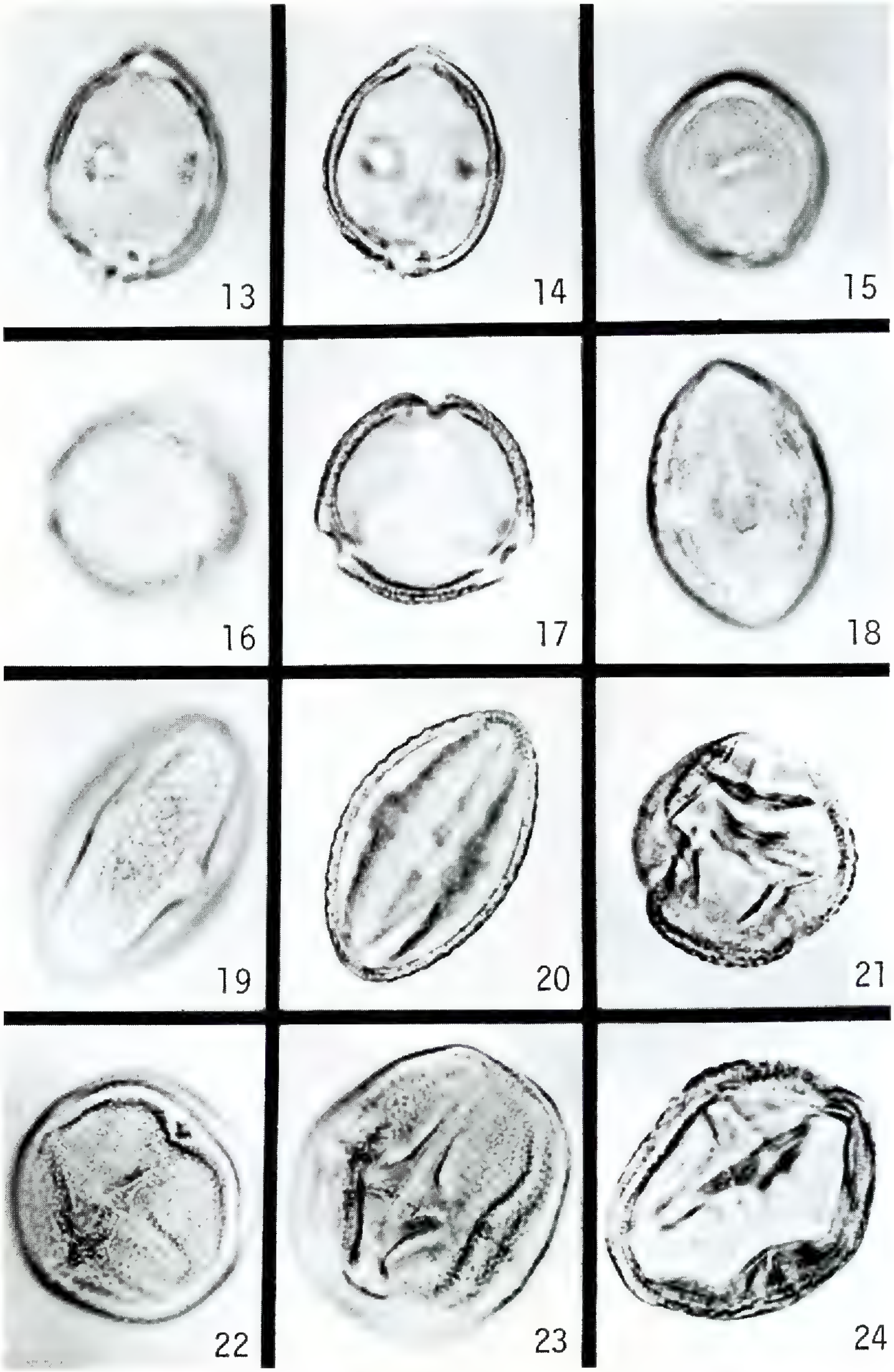
Aperture. Brevitricolporate, colpus transversalis. Grains slightly aspidorate. When acetolyzed the colpus membrane formed by the nexine is modified. After acetolysis the remaining structure, the sexine, is psilate under the light microscope. With the SEM this structure is scabrate in unacetolyzed grains. Polar index, 0.7; colpus transversalis, 7 μm. $\times$ 3 μm.; colpi, 9.38 μm.; pore, 9 μm. $\times$ 4 μm.

Ornamentation. Tectum perforate to heteroreticulate; lumina 0.3–0.8 μm., distributed at random; muri simplibaculate. Stratification clear, colum-

[1] Arnold Arboretum of Harvard University, Cambridge, Mass.
[2] Gray Herbarium of Harvard University, Cambridge, Mass.



FIGURES 1–12. 1–5, *Apeiba tibourbou* (from *Pennington & Sarukhán 9065*, Tuxtepec, Oaxaca, México), × 1000. 1, 2, polar view: 1, high focus; 2, median optical section. 3–5, equatorial view: 3, high focus (note brevicolporate aperture); 4, optical section (note effect of acetolysis on sexine of os); 5, broken grain showing well-developed colpus transversalis in compound aperture. 6–10, *Belotia mexicana* (from *Pennington & Sarukhán 9278*, Puebla, México), × 1000. 6, polar view, high focus. 7–10, equatorial view: 7, high focus (colpus transversalis covered by the sexine); 8, high focus (colpus transversalis complete); 9, high focus; 10, optical section. 11, 12, *Carpodiptera ameliae* (from *Matuda s.n.*, Tenosique, México), × 1000, polar view: 11, high focus; 12, median optical section.



FIGURES 13–24. 13–15, *Carpodiptera ameliae* (from *Matuda s.n.*, Tenosique, México), × 1000, equatorial view: 13, high focus; 14, optical section; 15, high focus. 16–20, *Heliocarpus donnell-smithii* (from *Matuda s.n.*, Acocoyagua, Chiapas, México), × 1000. 16, 17, polar view: 16, high focus; 17, median optical section. 18–20, equatorial view: 18, 19, high focus; 20, median optical section. 21–24, *Luehea speciosa* (from *Martínez-Calderón 201*, Tuxtepec and vicinity, Oaxaca, México), × 1000: 21, polar view, optical section on one side and high focus on others; 22, 23, high focus; 24, optical section (note clear stratification of sexine on one side of grain).

ellae easily seen. Exine, 1.5 μm. (ectosexine, 0.5 μm., endosexine, 0.75 μm., nexine, 0.25 μm.).

Belotia mexicana (DC.) K. Schum. FIGURES 6–10, 26, 32.

APERTURE. Tricolporate, colpus transversalis. The colpus membrane is psilate when the grain is acetolyzed, but verrucae are present close to the colpus transversalis. Without acetolysis the colpus membrane is scabrate (SEM sample). Polar index, 0.2; colpus transversalis, 24 μm. × 6.8 μm.; colpi, 25.04 μm.; pore, 3.82 μm.

ORNAMENTATION. Semitectate, supraheterobrochate. Lumen size decreasing toward the apertures. There is a wide range between the sizes of the lumina (0.3–0.8 μm.). Stratification clear; muri simplibaculate. SEM photographs show the tectum to be perforate within the lumina. Columellae visible. The nexine disappears at the level of the colpus transversalis. The ornamented sexine remains when the grains are acetolyzed. Exine, 1.6 μm. (ectosexine, 0.4 μm.; endosexine, 0.8 μm.; nexine, 0.4 μm.).

Carpodiptera ameliae Lundell. FIGURES 11–15, 27, 33.

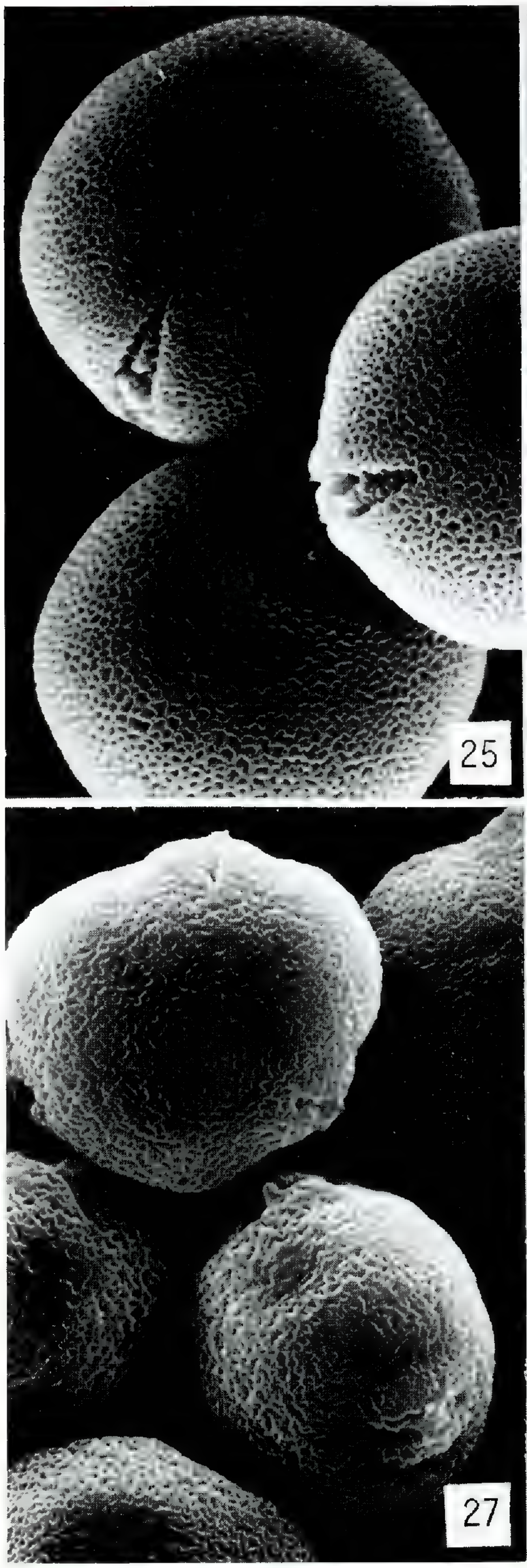
APERTURE. Tri-brevicolporate and tetra-brevitricolporate (less frequently). Aspidorate. Pore oval, meridianally elongated. Pore membrane scabrate when acetolyzed (light microscope sample). Before acetolysis the grains have a notch located in the ora region of the aperture. This notch is lost upon acetolysis, and instead it is possible to see an exoaperture. Unacetolyzed grains are endoaperturate. The membrane of the colpi is psilate (acetolyzed grains). There is a homogeneous layer constituting the endosexine at the pore level. Polar index, 0.7; colpi, 4.25 μm.; pore, 1.89 μm.

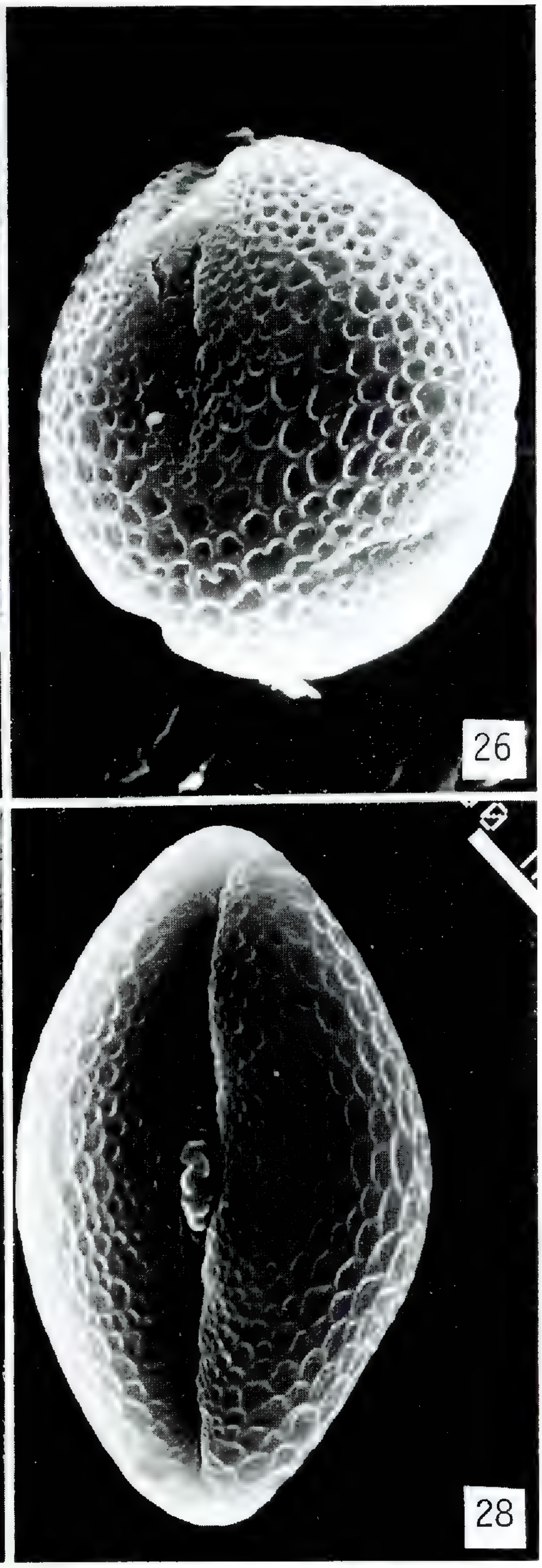
ORNAMENTATION. Infratectate, perforate, microreticulate when acetolyzed (light microscope sample). Fossulate when unacetolyzed (SEM sample) (Walker & Doyle, 1975), microrugulate. Muri simplibaculate. Exine 1.6 μm. The ratio between the ectosexine, the endosexine, and the nexine is 1:2:1.

Heliocarpus donnell-smithii Rose. FIGURES 16–20, 28, 29, 34.

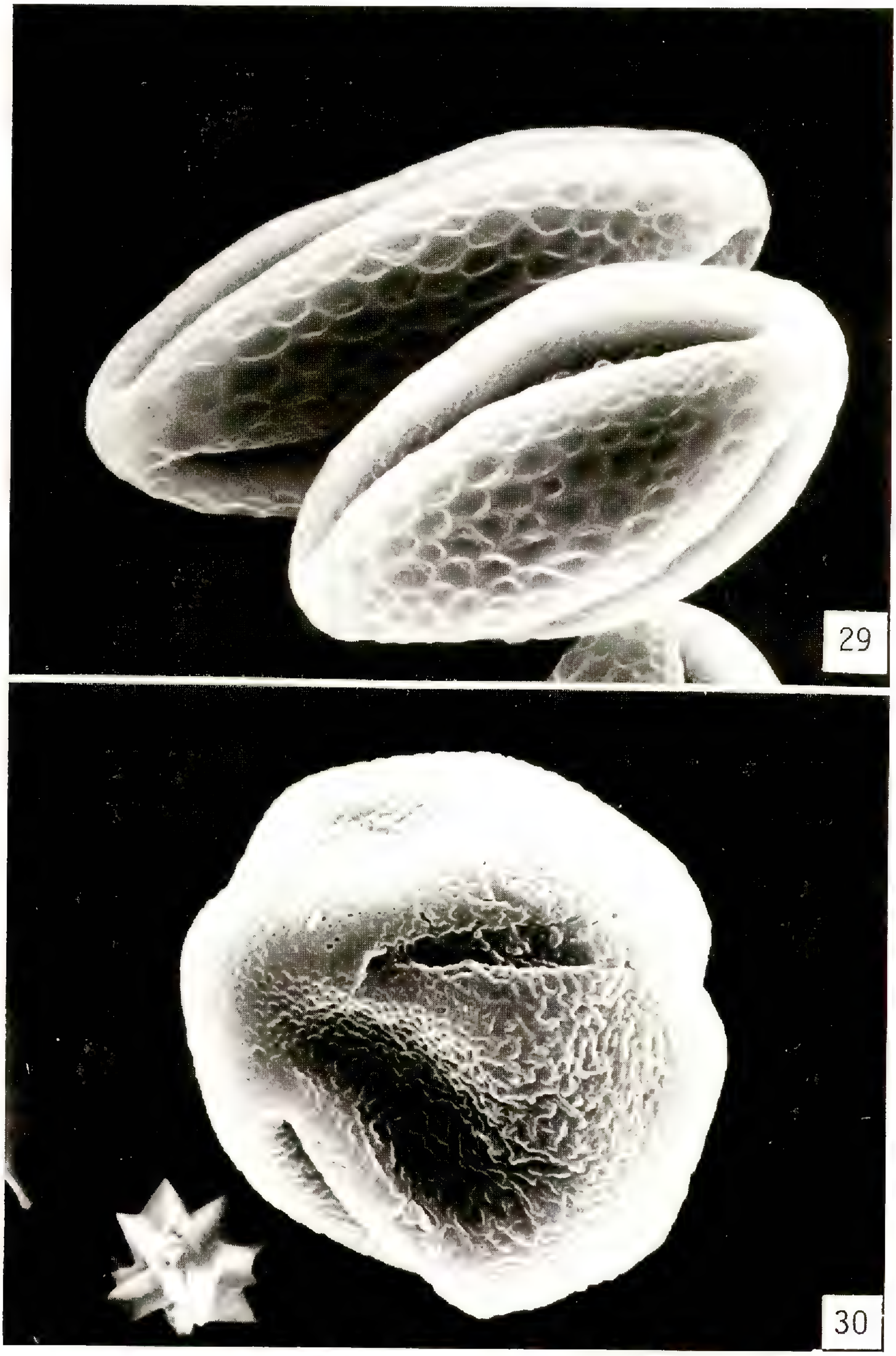
APERTURE. Tricolporate, endoaperturate. Colpus membrane psilate (acetolyzed grains). The grains have a notch placed at the ora of the colpus when they are unacetolyzed. The pore is anisodiametric, oval, meridianally elongated. Polar index, 0.2; colpi, 29.24 μm.; pore, 4.32 μm. × 6 μm.

ORNAMENTATION. Tectate, supraheteroreticulate. Two classes of lumina are found. The first kind decreases in size toward the aperture; the second is smaller and is distributed uniformly across the surface among those of the first type. Muri simplibaculate. The tectum is perforate inside the lumina (SEM sample). Columellae are easily seen. At the level of the pores, the ectosexine is thin, while the endosexine is thick. Exine, 1.6 μm. (ectosexine, 0.3 μm.; endosexine, 0.8 μm.; nexine, 0.5 μm.).

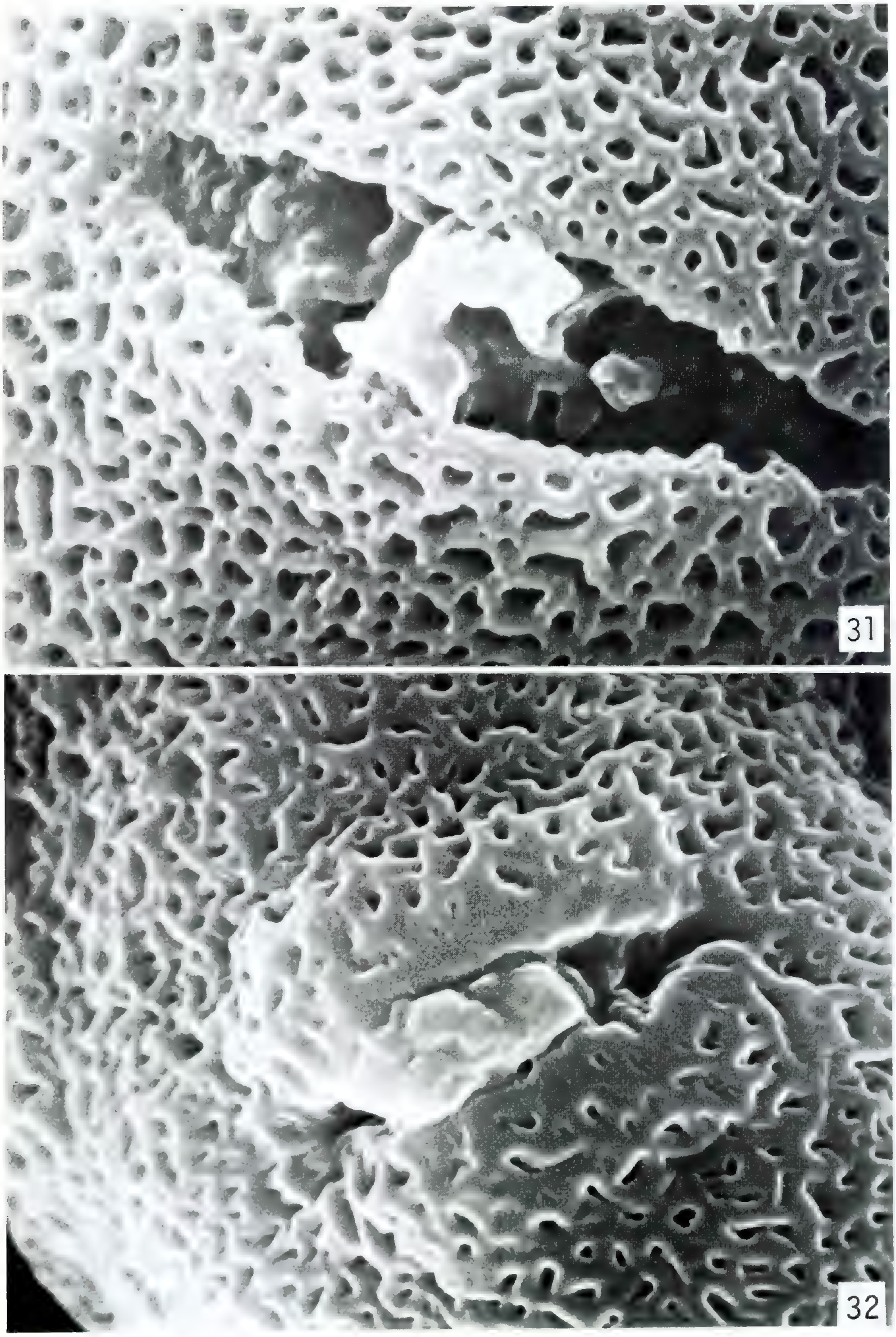




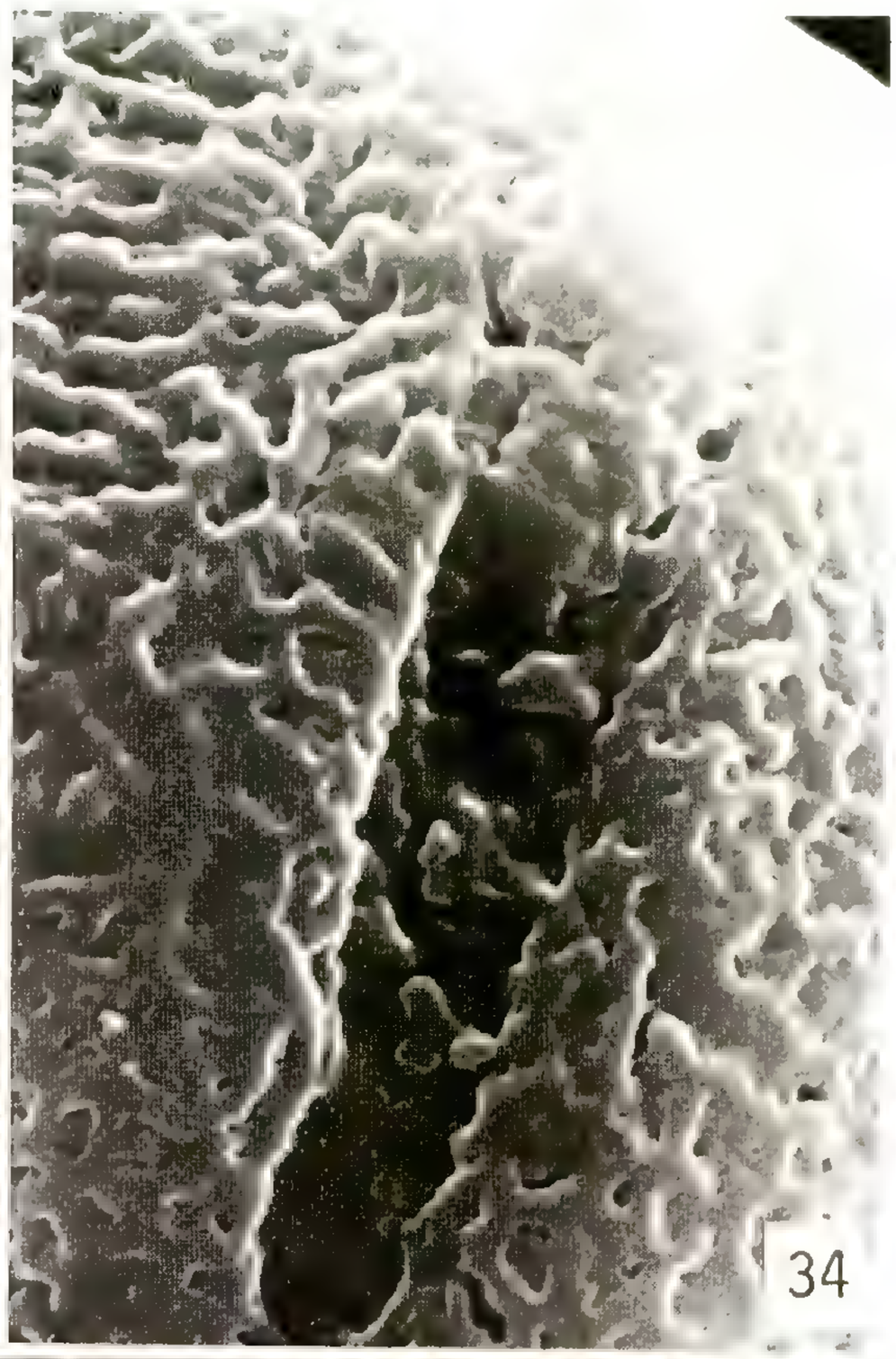
FIGURES 25–28. Scanning electron micrographs of pollen grains: 25, *Apeiba tibourbou* (from *Dressler & Jones 211*, Veracruz, México); 26, *Belotia mexicana* (from *Pennington & Sarukhán 9278*); 27, *Carpodiptera ameliae* (from *Matuda 3626*, Tabasco, México); 28, *Heliocarpus donnell-smithii* (from *Martínez-Calderón 452*, Tuxtepec, Oaxaca, México); all × 2000).

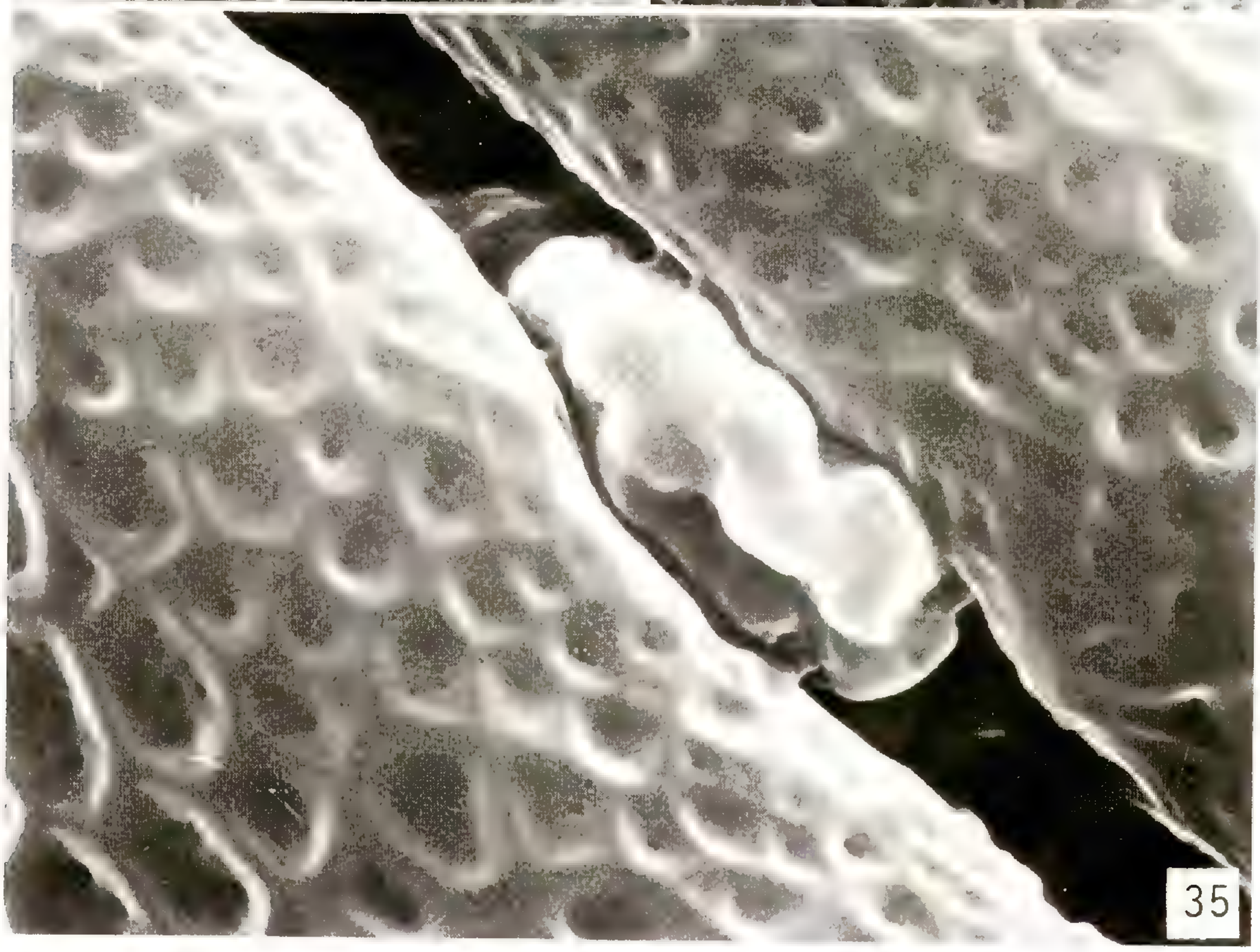


FIGURES 29, 30. Scanning electron micrographs of pollen grains: 29, *Heliocarpus donnell-smithii* (from *Martínez-Calderón 452*); 30, *Luehea speciosa* (from *Purpus 1917*, Veracruz, México); both × 2000.



FIGURES 31, 32. Scanning electron micrographs of pollen grains: 31, *Apeiba tibourbou* (from *Dressler & Jones 211*), × 10,000; 32, *Carpodiptera ameliae* (from *Matuda 3626*), × 5000.





FIGURES 33–35. Scanning electron micrographs of pollen grains: 33, *Belotia mexicana* (from *Pennington & Sarukhán 9278*), × 10,000; 34, *Heliocarpus donnell-smithii* (from *Martínez-Calderón 452*), × 10,000; 35, *Luehea speciosa* (from *Purpus 1917*), × 50,000.

Luehea speciosa Willd. FIGURES 21–24, 30, 35.

APERTURE. Tricolporate. Colpus membrane scabrate (SEM sample). Colpus transversalis 14–16 μm. long and 4–5 μm. wide. Polar index, 0.4; colpi, 23.92 μm.; pore, 5.93 μm. The unacetolyzed grains have a notch at the ora of the colpus that is lost during acetolysis.

ORNAMENTATION. Tectate, supraheteroreticulate. Lumina of the supratectum measure from 0.8 to 1.4 μm. Rugulate (SEM sample). Muri simplibaculate; columellae easily seen. Exine, 1.6 μm. (ectosexine, 0.4 μm.; endosexine, 0.8 μm.; nexine, 0.4 μm.).

DISCUSSION

The species of Tiliaceae studied are, in general, tricolporate. Using this feature we can determine two groups among the species observed: (1) brevitricolporate (*Apeiba tibourbou* and *Carpodiptera ameliae*), and (2) tricolporate (*Belotia mexicana*, *Heliocarpus donnell-smithii*, and *Luehea speciosa*). The pollen grains of *C. ameliae* can also be tetracolporate.

In all except *Carpodiptera ameliae* and *Heliocarpus donnell-smithii*, the aperture is a colpus transversalis (Faegri & Iversen, 1964). They have in common a colpus membrane constituted by the endexine. *Carpodiptera ameliae* has a pore membrane in addition to the other structures. *Heliocarpus donnell-smithii* and *Carpodiptera ameliae* are endoaperturate.

The pollen grains of these species were studied after two different treatments, with and without acetolysis. This produced remarkable differences between the apertures and ornamentation of grains of the same species (see text). The apparent changes were actually the result of loss of structures that had obscured other characters.

The polar index, besides other features, seems to be important as a distinguishing character. We found a correlation between the polar index and the form of the grains.

Depending on the structure, there are tectate grains (*Apeiba tibourbou*) or semitectate grains (*Belotia mexicana*); some may have supraornamentation (e.g., *Belotia mexicana*).

The width of the exine is very uniform, but differences occur in the ectosexine-endosexine-nexine ratio.

Sizes of the different structures, as well as shape, association, polarity, and symmetry, are shown in TABLE 1.

SUMMARY

Although the Tiliaceae has representatives in the temperate zone that have been well studied, the representatives of the family in the tropics have been ignored from the palynological standpoint. They are very important as components of tropical ecosystems. For this reason we have studied their pollen morphology, and that of some of the more important elements of tropical tree flora of Mexico.

TABLE 1. Pollen characteristics of five species of Tiliaceae.

	Apeiba tibourbou		*Belotia mexicana*		*Carpodiptera ameliae*		*Heliocarpus donnell-smithii*		*Luehea speciosa*	
Size	mean (μm.)	range (μm.)	mean (μm.)	range (μm.)	mean (μm.)	range (μm.)	mean (μm.)	range (μm.)	mean (μm.)	range (μm.)
POLAR AXIS	24.8	24 –26	34.64	32.8–38.4	20.8	16 –22	32.96	28 –36.8	30.56	24 –40
EQUATORIAL AXIS	33.43	28.8 –36.4	29.82	26.4 32.4	25.02	22.8 –28	23.72	20 –30.4	22.82	19.8–25.02
LUMINA	0.5	0.3 – 0.8	–	0.3– 0.8	0.4	–	1.51 (large lumina)	1.2– 2	0.5	0.4 0.6
							0.8 (small lumina)	0.6– 1		
COLPI	9.38	8 –12	25.04	20 –28.8	4.25	4 – 6	29.24	25.2–34.4	23.92	16.8 28.8
PORES	1.89	1.2 –24	3.82	2 – 5.6	1.89	1.2 – 2.4	4.32	3.2– 5.2	0.76	0.4 - 2.8
COLPUS TRANSVERSALIS	9.5 × 4.0	9 –10 long	24 × 6.8	–	–	–	–	–	15 × 4.5	14 –16 long 4 – 5 wide
EXINE: ECTOSEXINE	0.5	–	0.4	–	0.4	–	0.3	–	0.4	–
ENDOSEXINE	0.75	–	0.8	–	0.8	–	0.8	–	0.8	–
NEXINE	0.25	–	0.4	–	0.4	–	0.5	–	0.4	–
Shape	oblate		prolate		oblate		prolate		prolate	
Association	monad		monad		monad		monad		monad	
Polarity	isopolar		isopolar		isopolar		isopolar		isopolar	
Symmetry	radial		radial		radial or bilateral		radial		radial	

Five species in five different genera are included in this paper: *Apeiba tibourbou*, *Belotia mexicana*, *Carpodiptera ameliae*, *Heliocarpus donnell-smithii*, and *Luehea speciosa*. All of them are tricolporate but some are brevitricolporate, indicating variability in the polar index. The ornamentation and structure of pollen in the species studied appear to be characteristic of the genera.

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We would like to thank the several members of the staff at Harvard University who made the realization of this paper possible. Special thanks are due to Dr. Alice Tryon for her valuable assistance. Also we would like to thank Professor R. M. Tryon, Professor E. S. Barghoorn, B. Tiffney, E. Seling, of the Museum of Comparative Zoology, and the Arnold Arboretum-Gray Herbarium library personnel.

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Journal of the Arnold Arboretum *July, 1978*

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COVER: The stylized representation of fruits of various Leguminosae, forming the design of our new cover for Volume 59, is based on material from plants growing in the Arnold Arboretum of Harvard University. The design was planned and executed by Karen S. Velmure, who has also drawn several of the preceding covers as well as various devices used in the *Journal of the Arnold Arboretum* and on the offprint covers.

The three subfamilies of the Leguminosae are represented by the fruits shown in the design. The genera are, top row (left to right), *Albizia* (Mimosoideae), *Gleditsia* (Caesalpinioideae), *Caragana* (Faboideae), *Gymnocladus* (Caesalpinioideae), and lower row, right, *Colutea* (Faboideae).

The family Leguminosae, the second most important family of flowering plants, is to be the subject of an International Legume Conference at the Royal Botanic Gardens, Kew, Richmond, Surrey, England, in July, 1978. This cover is our salute to the complete success of that Conference.

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JOURNAL
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GENERIC LIMITS IN THE TRIBE CLADOTHAMNEAE (ERICACEAE), AND ITS POSITION IN THE RHODODENDROIDEAE

BRUCE A. BOHM, SCOTT W. BRIM, RICHARD J. HEBDA, AND P. F. STEVENS

THE CLADOTHAMNEAE COMPRISE a group of four species, all ornamental shrubs, in the Ericaceae subfamily Rhododendroideae. Although they are all fairly well known, being in cultivation, the four species have been given four generic names. There is no consistency in the usage of these names, as the arrangements listed below indicate.

	SPECIES EPITHET	*racemosa*	*paniculata*	*bracteata*	*pyroliflorus*	REFERENCE
GENERIC PLACEMENT		***Elliottia***	***Elliottia***	***Elliottia***	*Cladothamnus*	Hooker, 1876; Copeland, 1943
		Elliottia	***Elliottia***	*Botryostege*	*Cladothamnus*	Stapf, 1934
		Elliottia	*Tripetaleia*	*Tripetaleia*	*Cladothamnus*	Drude, 1897; Cox, 1948
		Elliottia	*Tripetaleia*	*Tripetaleia*	*Tripetaleia*	Stevens, 1971 (combination of *C. pyroliflorus* in *Tripetaleia*, not published)

In the following discussion, Copeland's nomenclature will be followed.

This paper is an attempt to resolve the generic limits in the group by using evidence from anatomy, chemistry, morphology, and palynology,[1] and combining this information with what is already known about floral anatomy. The evidence presented here suggests that there is only a single

[1] The sections of morphology and anatomy are by Brim and Stevens; the former examined the group during the course of his work for a Senior Thesis at Harvard University. Bohm has a long-standing interest in the flavonoids of the group, while the pollen was examined by Hebda in conjunction with the work of the other authors. The introduction and general discussion, written by Stevens, are acceptable to all.

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genus, *Elliottia*, and it also provides a firmer basis for understanding the phylogeny of the Ericaceae subfamily Rhododendroideae as a whole.

The Cladothamneae were first recognized as a separate tribe within the Rhododendroideae by Copeland (1943) on the basis of evidence from morphology, floral anatomy, and embryology. Four species were included: *Cladothamnus pyroliflorus* Bongard, from northwestern North America (MAP 2); *Elliottia racemosa* Muhl. ex Elliott, from southeastern North America (MAP 3); and *E. paniculata* (Siebold & Zucc.) Bentham & Hooker f. and *E. bracteata* (Maxim.) Bentham & Hooker f., both from Japan (MAP 1). A fifth species, *Tripetaleia yakusimensis* Nakai, has been described from Japan, but it was considered by Kyôgoku (1962) to be a synonym of *T. paniculata* Siebold & Zucc. (*E. paniculata*). On the basis of numerical analysis, Watson, Williams, and Lance (1967) suggested that the species that they studied (*C. pyroliflorus*, *E. paniculata*, and *E. bracteata*) would be better included in the Rhodoreae D. Don. Stevens (1971) followed Copeland in his circumscription of the Cladothamneae. Whether placed in a separate tribe or not, the four species included in the Cladothamneae are clearly more closely related to one another than they are to any other members of the Rhododendroideae.

Ericaceae subfamily Rhododendroideae tribe **Cladothamneae** Copeland.

Shrubs or small trees. Indumentum of unicellular hairs only, plant sometimes almost glabrous. Leaves deciduous, convolute in bud, entire. Inflorescence terminal, ± monotelic (cymose), eperulate; ± foliaceous bracts and "bracteoles" usually present, the former sometimes occurring alone, without the latter; pedicel continuous with the calyx. Flowers 3- to 5-(or 6-)merous; calyx well developed, the sepals connate or free; corolla polypetalous; stamens 5 to 10, the filaments flattened, the anthers with resorption tissue, dehiscing by long slits, the pollen shed in very young bud, the tetrads with viscin threads; ovary glabrous, 3- to 5-locular, placentation axile, the placentae apical; style impressed into the apex of the ovary, with an expanded collar around the ± prominent stigma. Capsule septicidal; seeds variable in size and shape, the cells of the testa thin walled, polygonal, with large pits (3–)6–15 μm. across, the embryo with a poorly developed chalazal haustorium. TYPE: *Cladothamnus* Bongard.

GROWTH, MORPHOLOGY, AND ANATOMY

VEGETATIVE ORGANS

GROWTH AND MORPHOLOGY. Like most of the Ericaceae, the four members of the Cladothamneae prefer acid habitats. *Elliottia bracteata*, *E. paniculata*, and *Cladothamnus pyroliflorus* are shrubs less than three meters tall, and, although *E. racemosa* is apparently at least initially a tree, Knight (1938) noted that most plants in the wild are shrubby because they sprout vigorously from the base after damage. All taxa have the same basic architecture: the stems are basically orthotropic, each shoot is terminated

by an inflorescence, and growth is continued by the development of axillary buds. This growth pattern basically conforms to Leeuwenberg's model (nomenclature that of Hallé & Oldeman, 1970) and is similar to that of many Ericaceae, especially the great majority of the subfamily Rhododendroideae (Temple, 1975).

Shoots of the four species can readily be distinguished from one another, even in winter, although the differences between them are mostly trivial. The bark of *Cladothamnus pyroliflorus* begins to exfoliate on twigs that are one year old; this character is not nearly so marked in other species, although in all the phellogen is initiated inside the ring of pericyclic fibers of the stem. *Elliottia paniculata* has sharply angled twigs, the angles being decurrent from the bases of the leaves; the twigs of *E. racemosa* are almost terete (the inflorescence less so); the other two species are intermediate. Not surprisingly, *E. paniculata* has the most prominent foliar buttresses.

The vegetative buds of *Elliottia racemosa* and *Cladothamnus pyroliflorus* consist simply of paired, mucronate bud scales. However, in *E. bracteata*, and even more so in *E. paniculata*, the outer pair of scales does not enclose the mucronate inner scales, so the bud scales are imbricate.

All species have inflorescences terminating the current year's growth, and the terminal buds of vegetative shoots are functional; there is, however, rather surprising variation in the growth patterns of the four species. Often in *Elliottia paniculata*, less frequently in *E. bracteata*, very rarely and perhaps only exceptionally in *E. racemosa*, and never, apparently, in *Cladothamnus pyroliflorus*, growth of the vegetative shoot ceases after a few weeks, and a more or less perulate terminal resting bud, with prominent and well developed scales, is formed (e.g., see Nakai, 1922, under *Tripetaleia paniculata*). Growth soon starts again, and small leaves and an inflorescence are produced (FIGURE 1, D).

In the two other species of the Cladothamneae, *Elliottia racemosa* and *Cladothamnus pyroliflorus*, there is usually no obvious cessation of plant growth, and the foliage leaves and bracts are not clearly distinguishable. However, in *E. racemosa* elongation of the main axis slows down soon after the axis is initiated and then speeds up again. In *E. bracteata* the growth of the inflorescence is frequently similar to that of *C. pyroliflorus* (but see above), although specimens placed in *Elliottia* (*Tripetaleia bracteata* var. *longiracemosa* Nakai) suggest that the transition between vegetative growth and the growth of the inflorescence may sometimes be abrupt (FIGURE 1, B). In these specimens the leafy vegetative shoot has large buds in the axils of the leaves and is rather clearly distinct from the inflorescence, which is long, the lower 4.5–7(–10) cm. of the axis bearing small leaves in the axils of which are neither flowers nor obvious buds. In *E. paniculata* and *E. bracteata* both continuous and discontinuous growth may occur on a single plant during the same season.

The growth pattern of *Elliottia racemosa* and *E. bracteata* has not been observed before in the Ericaceae and may be unique in the family (a comparative study of growth patterns and inflorescence type and develop-

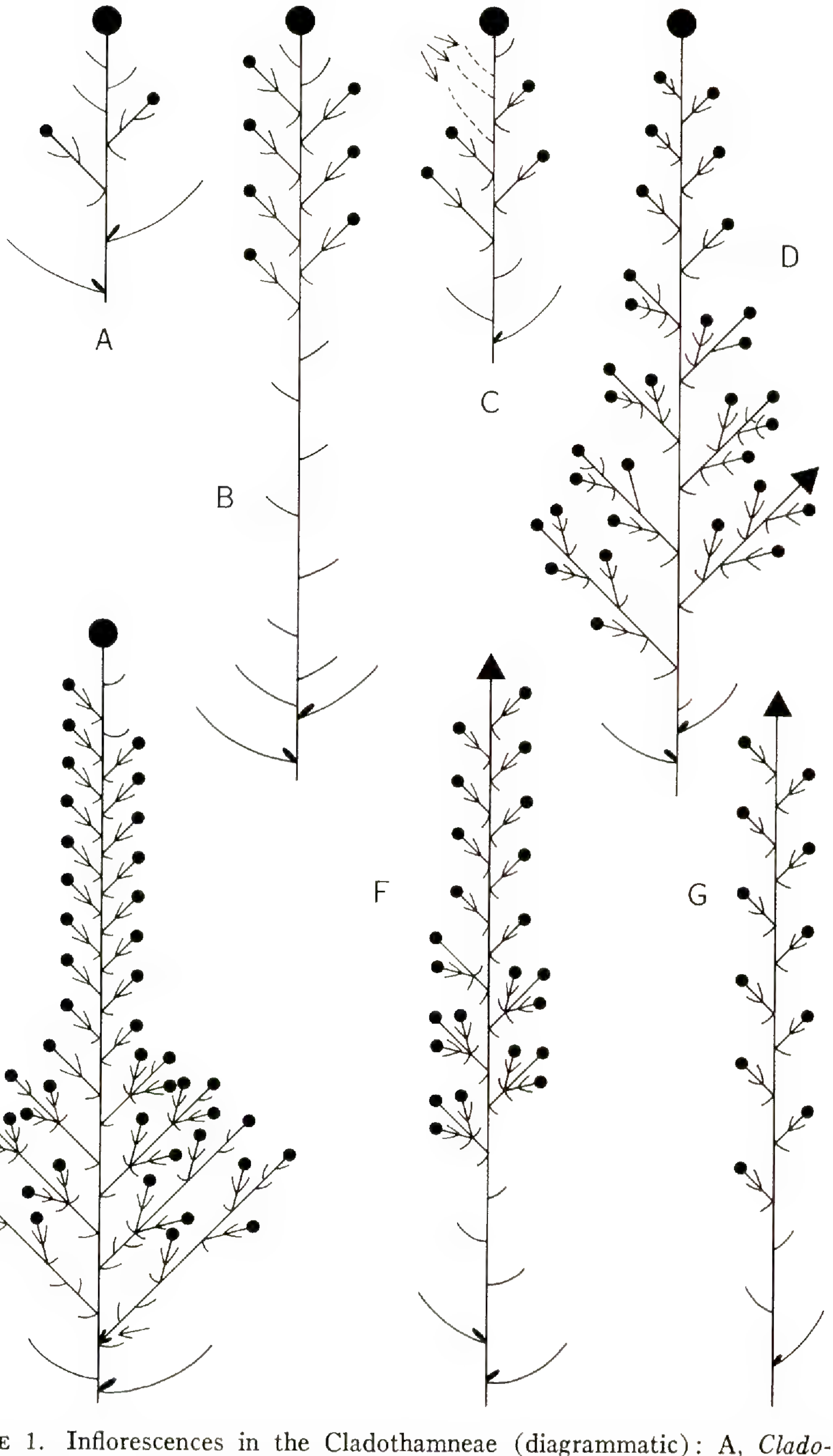

FIGURE 1. Inflorescences in the Cladothamneae (diagrammatic): A, *Cladothamnus pyroliflorus*; B, *Elliottia bracteata* var. *longiracemosa*; C, *E. bracteata* (normal); D, *E. paniculata*; E, *E. bracteata*, unusual branched inflorescence; F, G, *E. racemosa* (circles indicate flowers; ellipses, buds; triangles, axis not obviously terminated by a flower).

ment (see below) throughout the family is much needed). Although Lems's (1962) interesting study of shoot development in the Andromedeae did not include a similar pattern, the closest approach to it seems to be in that tribe. In *Pieris japonica* (Thunb.) D. Don a leafy shoot, a resting bud, and then another leafy shoot terminated by an inflorescence are frequently all produced in the same season; however, the flowers of the inflorescence do not open until the following year (W. Judd, pers. comm.).

All four species of the Cladothamneae are deciduous. (Stevens, 1971, reported that *Elliottia racemosa* was evergreen, but the living plant observed was growing in a greenhouse.) The leaves of *E. racemosa* have long petioles, while those of *Cladothamnus pyroliflorus* are sessile; the other two species have leaves with at most short petioles. Distribution of indumentum and the shape and texture of the leaf blade allow each species to be recognized by its leaf alone (see Key).

ANATOMY. The wood anatomy of *Elliottia racemosa*, *E. paniculata*, and *Cladothamnus pyroliflorus* was examined by Cox (1948). In this respect, *E. racemosa* was found to be more distinct from the other two species than the two species were from each other. In *E. paniculata* there was a slight preponderance of scalariform perforation plates with more than nine bars, and there were round pits in the wood parenchyma and on the side walls of the vessels. In the other two species there was a strong preponderance of perforation plates with fewer than eight bars, the pits were round or elongate-elliptic, and there were also differences in medullary ray type. *Elliottia racemosa* and *C. pyroliflorus* were similar, differing mainly in the percentage of vessels with porous perforation plates. However, it is difficult to evaluate the significance of these differences since the variation between the species that Cox considered in the natural genus *Befaria* Mutis ex L. was as great as that between the three species of the Cladothamneae that he examined. Perhaps, more importantly, many of the characters that Cox used both vary infraspecifically and also depend on the age and the general health of the part of the plant from which the material examined was taken (see Carlquist, 1961, for references).

The pith of all four species is heterogeneous, with clusters of thick-walled cells interspersed with clusters of larger, thin-walled cells. (Watson, 1965; Stevens, 1971; Gris, 1870, 1872; and Copeland, 1943, give descriptions of the pith that are in basic agreement.) However, the thick-walled cells toward the periphery of the pith tend to be especially well developed. This is particularly marked in *E. paniculata*, in which the pith approaches the *Calluna* type, with small, thick-walled cells in the periphery and larger, thin-walled cells restricted to the center. Copeland (1943) found that in *E. racemosa* most of the pith consisted of thick-walled cells, the thinner-walled cells being relatively inconspicuous.

Stevens (1971) noted that the vascular bundle in the petiole of *Elliottia racemosa* is closed, with the phloem surrounding a ring of xylem, while that of the other species was arcuate. However, in the smaller leaves of *E. racemosa*, especially those produced at the beginning of growth and

those produced later just below the inflorescence, the vascular bundle is open, although it is deeply arcuate. In some intermediate-sized leaves it may be open at the base of the petiole, but then it becomes closed higher up. In the other species it is always shallowly arcuate.

There are a number of differences in lamina anatomy between the four species. Most of these are relatively trivial, and include differences in the thickness of the cuticle, sinuosity of the anticlinal epidermal cell walls (an environmentally labile character), and length of the palisade mesophyll cells. All species have a single layer of palisade cells, although in *Cladothamnus pyroliflorus* and *Elliottia racemosa* there is often a more or less well-developed second layer. The variation in the shape of the midrib bundle mirrors that of the petiole: in *E. racemosa* it is closed to deeply arcuate, while in the other species it is shallowly arcuate. The stomata are always on the abaxial surface of the lamina. In *C. pyroliflorus* and *E. bracteata* the stomata are anomocytic, while in the other two species the majority of stomata are paracytic (Stevens, 1971). The cuticle in *E. bracteata* is almost reticulately ridged, while in the other species it is striate (most prominently so in *E. paniculata*) to smooth.

INFLORESCENCE

STRUCTURE. The inflorescences of the four members of the Cladothamneae are at first sight rather different one from another, and, with the partial exception of *Cladothamnus pyroliflorus*, they have often been called paniculate or racemose (i.e., polytelic: Hooker, 1876; Copeland, 1943; Wood, 1961; Stevens, 1971; Yamazaki, 1975). However, the inflorescences in all four species are basically similar and are more or less clearly monotelic (cymose). In the following discussion, unqualified use of the term "bract" will refer to a leafy structure on the main axis that usually subtends a first-order paracladium (a flower or a more complex, branched system that repeats the structure of the main axis of the flowering system); the bract may be empty. The term "second-order bract" will refer to a comparable structure on a first-order paracladium; and "third-order bract" to a leafy structure borne on a second-order paracladium. (This nomenclature follows that of Troll; see Weberling, 1965, for a convenient summary.)

Cladothamnus pyroliflorus (FIGURE 1, A) has the smallest inflorescence in the Cladothamneae. The 1- to 2- (to 4-)flowered inflorescence, a botrys, has bracts that are almost indistinguishable from the leaves, and any paracladia, which are always single flowers, have a pair of opposite to alternate second-order bracts that are usually called bracteoles because of their position. Between the paracladia and the terminal flower there are usually two or more bracts that do not subtend flowers; small buds are sometimes visible in the axils of these bracts. The terminal flower opens first.

Elliottia bracteata (FIGURE 1, C) has an inflorescence with essentially the same structure as that of *Cladothamnus pyroliflorus*, although the leafy

bracts are smaller and are more clearly distinguishable from the foliage leaves, and the inflorescence is larger, having 3 to 15 flowers. The terminal flower often opens first, although in larger inflorescences the lowest flowers open first, then the terminal flower, and, finally, the remaining ones. Between the two uppermost paracladia there is sometimes a bract lacking an axillant paracladium; this bract is out of phyllotactic sequence, as are any bracts above the uppermost paracladium. In other inflorescences the first bract that does not subtend a paracladium is inserted at, or almost at, the level of the uppermost paracladium, and in yet other inflorescences the first bract is inserted well above the uppermost paracladium (FIGURE 1, C, arrows). In these latter two cases regular phyllotactic sequence is maintained. In the first case the phyllotactic sequence would be regular if the first bract were inserted above the uppermost paracladium, so it seems that this first bract can be variable in position. In some inflorescences there are no empty bracts between the terminal flower and the uppermost paracladium.

Elliottia paniculata has a profuse, branched thyrse that may have over 40 flowers (FIGURE 1, D). The main axis of the inflorescence and the first-order paracladia terminate in flowers that open before the flowers immediately below them. The lower first-order paracladia of the inflorescence bear single flowers along their length and alternate second-order bracts between the terminal flower and the lateral flowers, while the upper first-order paracladia have more or less paired lateral flowers and usually lack second-order bracts between the terminal flower and the uppermost second-order paracladia. Where bracts are present between a terminal flower and a paracladium, they usually continue the phyllotactic spiral of the axis below them, although there is a tendency for the sterile first-order bracts on the main axis to be out of sequence (see above). All second-order paracladia have two subopposite third-order bracts and a terminal flower. The main axis or the first-order paracladium sometimes lacks terminal flowers, and instead there are a number of small bracts of the appropriate order as well as abortive paracladia (axillant flowers). In a few cases none of the paracladia has more than a single flower. When both such variations occur on a single inflorescence (terminal flower lacking only on the main axis), a "racemose" inflorescence results (see below, *E. racemosa*). The lowermost paracladium of one robust inflorescence of *E. bracteata* examined had a pair of second-order bracts, possibly bud scales, at its base (FIGURE 1, E, arrow). Vigorous, branched inflorescences on a plant of *E. bracteata* growing at the Arnold Arboretum were similar in structure to those of *E. paniculata* (FIGURE 1, E).

The main axis of *Elliottia racemosa* is usually not terminated by a flower, but there are a number of bracts subtending abortive paracladia toward the end. The only inflorescences we saw that were terminated by flowers were on a late-flowering plant at the Arnold Arboretum, but they apparently occur sporadically in nature (Wood, 1961, p. 22 (footnote)). The first-order paracladia have either a single terminal flower and two subopposite second-order bracts ("bracteoles": FIGURE 1, F), or two op-

posite second-order paracladia as well, these in turn having a terminal flower and two subopposite third-order bracts (FIGURE 1, G). More complex inflorescences have not been seen, and there are no bracts between terminal flower and paracladium on the lateral branches. The flowers toward the middle of the inflorescence open first (FIGURE 2, A), and the terminal flowers on the three-flowered branches in an inflorescence like that shown in FIGURE 1, G open before the lateral flowers (this latter has been observed before (e.g., Wood, 1961)).

Thus, the inflorescences of all four species are fundamentally monotelic (cymose), although they differ greatly in size and in overall appearance. The small, simple type of inflorescence of *Cladothamnus pyroliflorus* can be related to the more elaborate inflorescences of *Elliottia racemosa* and *E. paniculata* by the lengthening of the main axis, with the terminal flow-

FIGURE 2. Flower types in the Cladothamneae. A, B, *Elliottia racemosa*: A, inflorescence (note flowers in the middle of the inflorescence opening first); B, single flower (note ± erect petals and stamens). C, *E. bracteata* (note more or less spreading petals and stamens); D, *E. paniculata* (note spreading petals and filaments that are initially erect).

er consequently developing later and eventually not developing at all, and the development of both more and also higher orders of paracladia. The inflorescence shows a comparable trend in the reduction of foliation in both the bracts and the sepals. There is also a trend in the regularity of insertion of bracts on paracladia: in *C. pyroliflorus* the bracts tend to be alternate, but in *E. racemosa* they are rather strictly opposite.

Flower

Morphology. There are several differences between the members of the Cladothamneae in the numbers and arrangement of the parts of the flower (see Table 3). Some other floral differences are discussed below.

Calyx. The two species with free sepals, *Elliottia bracteata* and *Cladothamnus pyroliflorus*, also have a very much longer calyx than do the other two species (*E. bracteata*, ca. 5 mm. long; *C. pyroliflorus*, ca. 15 mm. long; *E. paniculata* and *E. racemosa*, less than 2 mm. long).

Corolla color. In *Elliottia racemosa* the petals are white, while in *E. paniculata* and *E. bracteata*, although basically white or pale greenish, they are more or less pink or streaked with pink toward the apex. The petals of *Cladothamnus pyroliflorus* are usually completely copper colored, although they are apparently sometimes greenish white (an albino form?).

Curvature of the stigma and protection of the nectary. Stevens (1971) noted that the petals of *Elliottia bracteata* (Figure 2, C) and *Cladothamnus pyroliflorus* were broadly spreading, as were the stamens. Insects visiting flowers of these species landed on the petals and flattened filaments and received pollen on their backs from that attached to the strongly curved stigma as they took nectar from the exposed nectary at the base of the flower. It was suggested that in *E. racemosa* and *E. paniculata* the pollination mechanism was similar, although it was noticed that petals of the former were not so reflexed; only herbarium material of the latter was seen.

Observations of vigorously growing plants of *Elliottia racemosa* and *E. paniculata* at the Arnold Arboretum show that the style is not strongly recurved and the nectary is not exposed. However, the method of nectar protection differs in the two species. In *E. racemosa* (Figure 2, B; Santamour, 1967, *fig. 54*) the petals are not particularly strongly reflexed and form a cup that encloses the nectary. The edges of the flattened filaments have spaces between them, and the filaments themselves are little bowed at their bases. In *E. paniculata* (Figure 2, D) the petals are reflexed and do not form a cup, but the filaments are bowed at their bases and in contact laterally, thus forming a tube around the base of the ovary and the nectary.

Some details of the pollination of *Elliottia racemosa* were given by Wood (1961), and, although field studies of the pollination of the Cladotham-

neae (and most other Ericaceae) are badly needed, the following additional information based on the plants growing at the Arnold Arboretum seems of interest. No visitors to *E. paniculata* or *E. bracteata* were seen, but numerous bees (*Bombus* and *Apis* spp.) were working *E. racemosa* (see also Santamour, 1967, *fig. 52*). When the pollen is shed in the young bud, it collects in the space between the petals and the stigma (the style is, as yet, short). The style elongates considerably in later bud and, just before the petals open, is compressed into an S-shape. The petals, with their somewhat hooded tips in which the stigma rests, tend to spring open violently when late buds are touched with twigs. Small masses of pollen held together by viscin threads were seen flying through the air when this happened; observations are needed to see if this is an important part of the pollination process. Visiting insects landed on and clung to the petals. The stigma, to which pollen is attached, touched the ventral and lateral surfaces of these insects as they probed for nectar between the filaments; the clefts on the stigmatic lobes are initially closed.

Seeds. The seeds of *Elliottia racemosa* are shieldlike; the embryo and endosperm occupy the central part and are surrounded by a wing composed of testa only (see Wood, 1961, for illustrations). The cells of the testa that forms the wing and that which covers the central part are similar, both having large pitted areas, and are similar to the testa cells of the other members of the Cladothamneae.

Pollen

Methods. For examination under the light microscope, pollen grains were first acetolyzed (Faegri & Iversen, 1964) and were then passed through an alcohol dehydration series before being mounted in silicone oil on glass slides. Measurements for each species were made on specimens from at least two different sources (see TABLE 1). Values were obtained for tetrad diameter, length of the furrow as exposed on the surface of the grain, width of the furrow margin, and exine thickness at the poles of grains.

Both acetolyzed and unacetolyzed pollen samples were prepared for SEM observation. Pollen was air-dried and mounted directly on copper conducting tape that was glued to an aluminum stub. Gold was evaporated onto the material in a Mikros model evaporator, and the stubs were then observed in a Cambridge stereoscan.

Results. The pollen of all four species is borne in tetrads (FIGURE 3, A). The range of tetrad diameter is 40–70 μm. (TABLE 1), with the diameters of these four species forming a series of overlapping ranges. *Elliottia paniculata* has the smallest tetrads, with means between 40 and 45 μm., whereas the other three species have tetrads with means between 40 and 55 μm. However, one of the two samples of *E. racemosa* (*Harper s.n.*) has larger tetrads that vary considerably in size, the mean diameter being 65.6 μm. Tetrad size is especially variable in this species; Santamour

Table 1. Variation in pollen measurements in the Cladothamneae.

	Elliottia bracteata*			Elliottia paniculata+		Elliottia racemosa°		Cladothamnus pyroliflorus++	
	1	2	3	4	5	6	7	8	9
Average tetrad diameter**	51.5	47.8	53.2	42.3	44.7	65.6	52.3	48.0	53.9
Range of tetrad diameter	45–59	44–52	51–57	36–50	42–48	59–74	47–60	42–54	49–57
Standard deviation	2.8	-	-	1.8	-	4.1	-	2.5	-
Sample size	100	10	25	100	10	27	102	100	10
Average grain diameter	35.1	35.2	35.0	30.7	30.0	47.9	37.2	33.0	36.0
Range of grain diameter	29–40	31–39	33–37	25–36	27–32	44–54	33–42	29–38	34–40
Standard deviation	2.1	-	-	2.3	-	3.4	-	2.0	-
Sample size	102	10	10	100	10	8	100	102	10
Furrow length	-	9.9	-	-	8.3	-	9.5	10.2	-
Margin width	-	3.6	-	-	3.9	-	4.3	4.4	-
Average exine thickness	1.2–1.6	1.2–1.6	1.2–2.0	1.6–2.0	1.6–2.0	1.6–2.4	2.0–2.4	2.0–2.4	1.2–2.0
Sample size	10	10	20	10	10	10	10	10	10

*Elliottia bracteata - 1. Bohm, 1975, Garden; 2, Faurie, 1905, Japan; 3, Muroi, 1955, Japan.

+Elliottia paniculata - 4, Bohm, 1975, Garden; 5, Muroi, 1955, Japan.

°Elliottia racemosa - 6, Harper, 1901, Georgia, U.S.A.; 7, Lee, 1960, Georgia, U.S.A.

++Cladothamnus pyroliflorus - 8, Bohm, 1975, B.C., Canada; 9, Peterson, 1959, B.C., Canada.

**All measurements in micrometers (μm.).

(1967) found less than 6 percent fertility in the material that he examined, and the collapse of one or two members of the tetrads was particularly noticeable in this study.

Furrow length (8.3–10.2 μm.) and margin width 3.6–4.4 μm.) are very similar for all four species. A pore extends equatorially to form a fusiform, transverse furrow (FIGURE 3, B) in all members of the group. The wide, differentiated border around the furrow (FIGURE 3, C) is formed mostly by a thickening of the endexine (FIGURE 3, D). This thickened area is surrounded by a peripheral endexinal crack (FIGURE 3, C, surface view; FIGURE 3, B, transverse view) which is usually connected to a network of endocracks (endexinal cracks: FIGURE 3, C) distributed over the visible surface of the grain.

The exine is semitectate, with the ektexine usually from 1.5 to 3 times thicker than the endexine. It consists of a thin foot layer and narrow columellae. Under high magnification both the light micrographs (FIGURE 3, E–H) and SEM micrographs show that the clavobaculate surface ornamentation is produced by the tops of the columellae, some of which are fused (FIGURE 4, B, D, F, H). *Elliottia racemosa* has slightly finer surface ornamentation (FIGURE 4, D) than do the other three species.

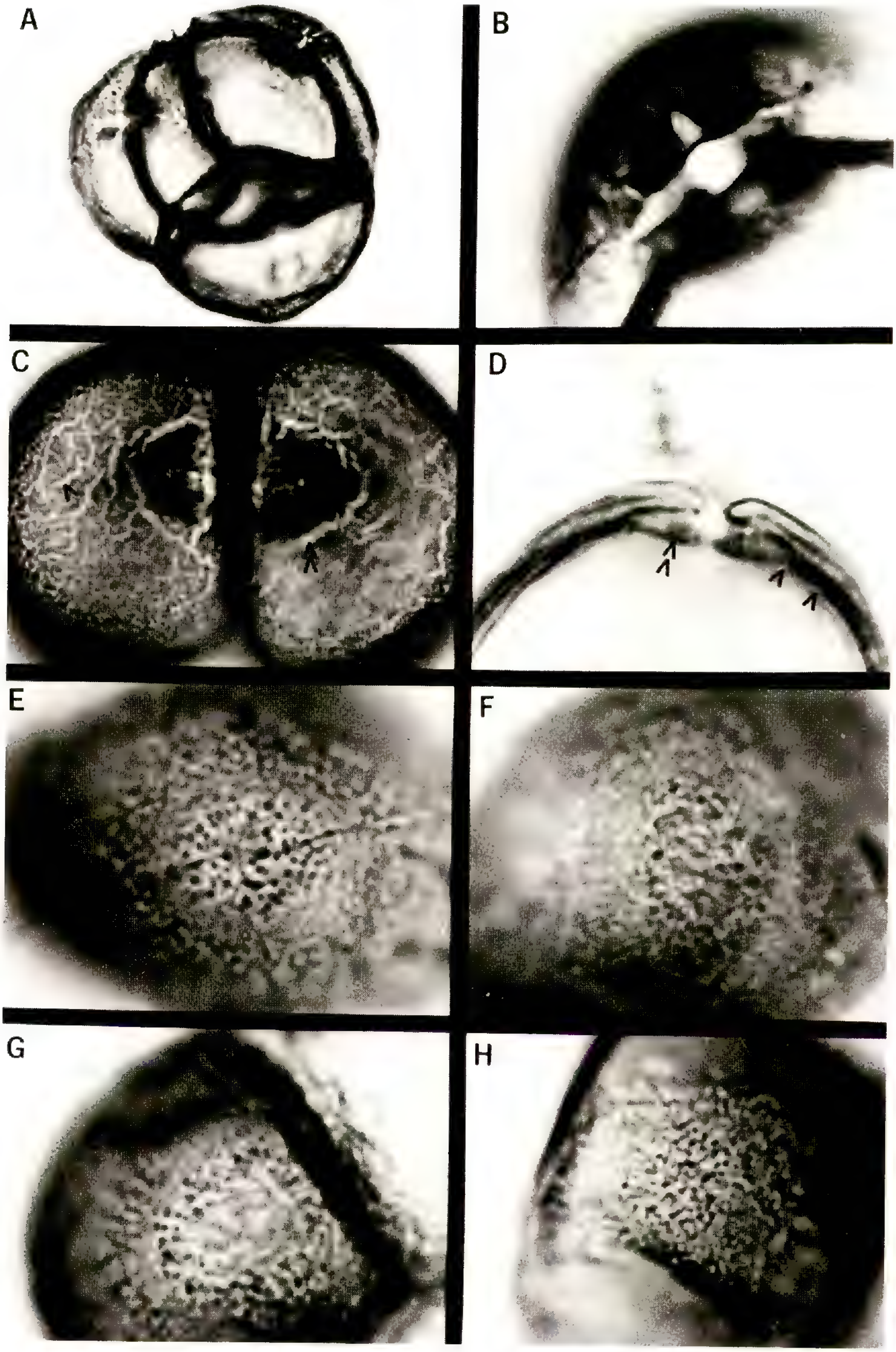

FIGURE 3. Details of pollen of the Cladothamneae. A, *Cladothamnus pyroliflorus*, tetrad, × 760; B, *Elliottia racemosa*, elongate pore crossing furrow, × 2000; C, *Elliottia bracteata*, surface of two adjacent furrows showing differentiated margins, with peripheral endexinal crack (double arrow) surround-

Exine thicknesses of *Elliottia racemosa*, *E. paniculata*, and *Cladothamnus pyroliflorus* are similar (means, 1.7–2.2 μm.), but the exine of the three collections of *E. bracteata* is somewhat thinner (means, 1.4, 1.4, and 1.5 μm.). Comparison of the SEM micrographs of the unacetolyzed tetrads (FIGURE 4, A, C, E, G) clearly shows that the tetrads of *E. bracteata* collapse much more severely than do those of the other species, probably because of this thinner exine. Collapse can also be seen under the light microscope and has already occurred in herbarium specimens. In some cases acetolysis somehow "reinflated" the grains, destroying the difference between *E. bracteata* and the other species.

The viscin strands observed earlier in the Cladothamneae (e.g., Copeland, 1943) can be clearly seen in the SEM photographs (FIGURE 4, A, C, E, G).

Conclusion. The pollen morphology is very similar in all four species. Although *Elliottia bracteata* has a somewhat thinner exine than do the other species, all of the other essential features are sufficiently similar to indicate very close relationships among the four species. Hence, pollen studies provide no evidence for placing the species in more than one group (see also General Discussion).

Cytology. Santamour (1967) reported a number of $n = 11$ for *Elliottia bracteata*.

Embryology. The chalazal haustoria in *Elliottia racemosa* and *Cladothamnus pyroliflorus* were essentially moribund according to Copeland (1942), and their absence was used to characterize the tribe. However, Yamazaki (1975) found small, but definite, chalazal haustoria in *E. paniculata* and *E. bracteata*. Dissection of mature seeds of *E. bracteata* showed a large micropylar haustorium (pers. obs., P. F. S.), although there was no trace of a chalazal haustorium. All species were reported to have a large micropylar haustorium. Any difference between the species in the size of the micropylar haustorium is probably one of degree only. The micropylar haustorium is much larger than the chalazal haustorium in all three species, whereas in most of the family both haustoria are prominent.

Anatomy. Copeland (1943) examined the floral anatomy of *Elliottia racemosa*, *E. paniculata*, and *Cladothamnus pyroliflorus*. In the first two species he found that there were separate traces to the individual sepals and petals; each of these traces later divided into three. The stamens were likewise supplied by single traces, and the carpels were vascularized by carpel dorsal, carpel ventral, and septal bundles. Branches of the carpel

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ing margins, and reticulum of endexinal cracks (single arrow), × 1248; D, *Elliottia paniculata*, transverse section of furrow, showing endexinal thickening (tip of double arrow) and two endexinal cracks (indentations at tips of single arrows), × 2000. E–H, surface ornamentation, heads of clavobacula showing as black spots, × 2000: E, *C. pyroliflorus*; F, *E. racemosa*; G, *E. paniculata*; H, *E. bracteata*. (For collections examined, see Figure 4.)

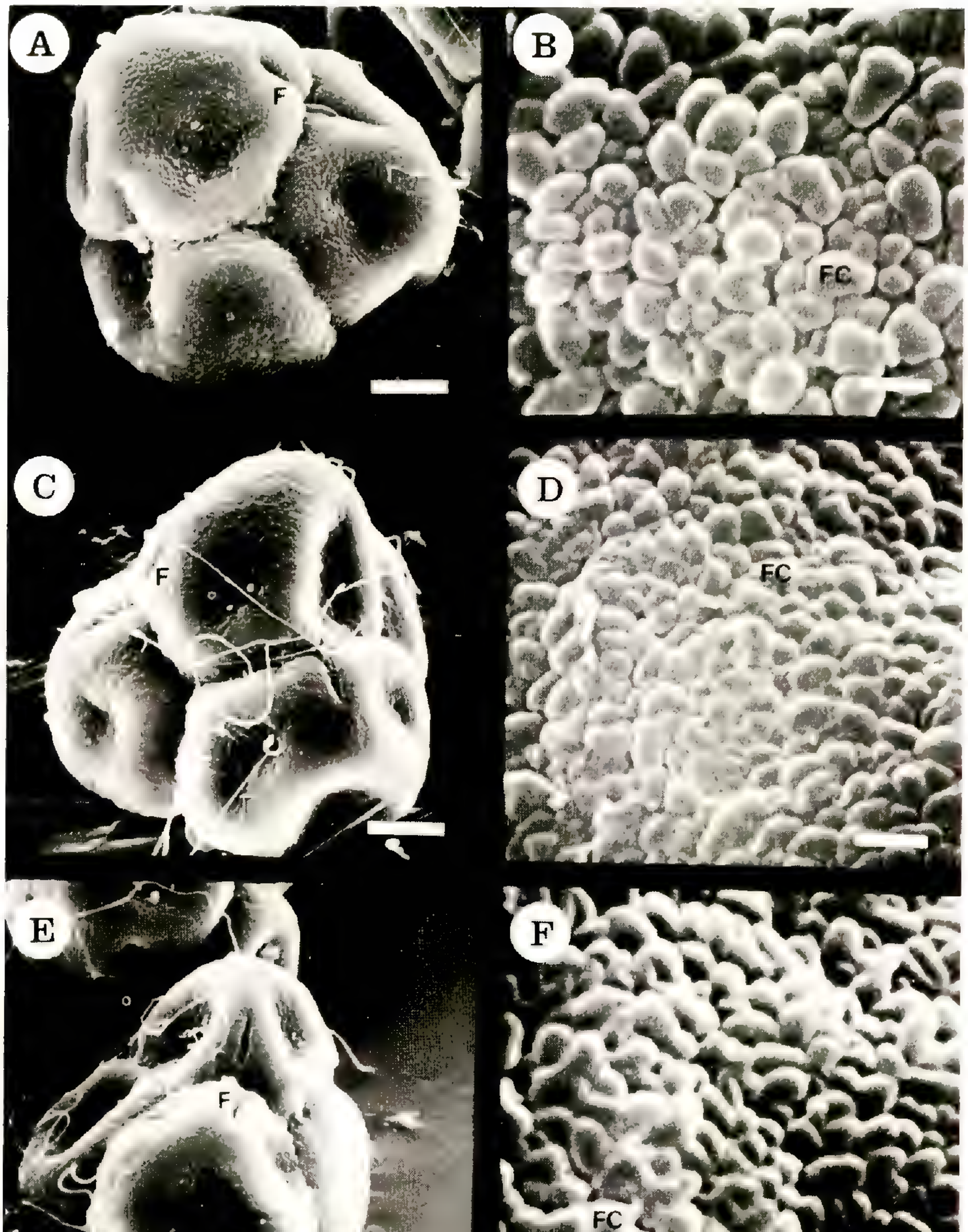

FIGURE 4. Comparison of the pollen of the Cladothamneae. A, C, E, G, scanning electron micrographs of pollen tetrads showing viscin strands and furrows

dorsal and the septal bundles vascularized the nectary. Copeland found *Cladothamnus pyroliflorus* to be basically similar, although its receptacle was depressed and the axis hence more compressed. Up to three vascular bundles supplied the sepals, with the lateral sepal bundles arising from other sepal bundles or from petal bundles, or even originating unattached in the receptacle. The bundles to the antepetalous stamens arose from the petaline bundles, while the vascular bundles supplying the antesepalous stamens sometimes originated from the main sepal bundle. The nectary was not vascularized.

Yamazaki (1975) recently examined the floral anatomy of *Elliottia bracteata* and *E. paniculata* (as *Tripetaleia*). His account disagrees in detail with that of Copeland (1943) and contains a novel suggestion concerning the origin of the petals in these two species. In *E. bracteata* Yamazaki found six petal traces arising from four gaps: two traces from adjacent gaps supplied the adaxial (upper) petal, while a pair of traces arose from each of the two lower gaps and entered the two abaxial (lower) petals. In *E. paniculata* he found that the adaxial petal was supplied by two traces from adjacent gaps, the abaxial petals being vascularized by a single trace that later forked into three. Other details were as given by Copeland (1943). In abortive flowers the upper petals frequently were supplied by a single bundle that forked into two; this bundle arose from a single gap. The vascular supply to the petals of *E. bracteata* suggested to Yamazaki that each petal might have been derived from two by fusion; the vascular supply of *E. paniculata* seemed to him to be more specialized than that of *E. bracteata*.

FLAVONOIDS

A few years ago a study of the flavonoids of the Cladothamneae was undertaken with a view to applying the data to the systematic problems within the tribe. The flavonoids of *Cladothamnus pyroliflorus* were determined at that time (Bohm & Saleh, 1972). Since then, material from the other three taxa has become available. *Cladothamnus* has been reexamined by improved methods, and the structures of the majority of flavonoids present in the other species have been determined.

Several reports of chemical constituents of members of the tribe have been published by other workers. Kondo *et al.* (1963) reported terpene derivatives, paraffins, fatty alcohols, and quercetin from *Tripetaleia paniculata* (= *Elliottia paniculata*). In a series of papers by Yasue and coworkers (1971a, 1971b, 1973, 1974; Sakakibara *et al.*, 1974), a number of long-chain fatty alcohols and ketones, sterol derivatives, simple phenolic

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(F), scale bar = 10 μm.; B, D, F, H, scanning electron micrographs of surface ornamentation of pollen grains, scale bar = 1 μm.: A, B, *Cladothamnus pyroliflorus* (from *Bohm*, 1975, B.C., Canada); C, D, *Elliottia racemosa* (*Lee*, 1960, Georgia, U.S.A.); E, F, *Elliottia paniculata* (*Muroi*, 1955, Japan); G, H, *Elliottia bracteata* (*Bohm*, 1975, garden). Note in G much greater collapse of tetrad in *E. bracteata*; in B, D, F, and H, fused clavobacula (FC).

compounds, and flavonoids were described from various tissues of the same species. The only flavonoid glycosides reported were quercetin 3-O-arabinoside and quercetin 3-O-galactoside. Harborne and Williams (1973) reported kaempferol, quercetin, and myricetin in hydrolyzed extracts of *Cladothamnus pyroliflorus* and *Elliottia racemosa* in their extensive survey of the Ericaceae.

Material. Cladothamnus pyroliflorus was collected in Mt. Seymour Provincial Park, British Columbia, Canada, at the site from which material was obtained for the earlier work on this species (Bohm & Saleh, 1972). *Elliottia racemosa*, from Bulloch Co., Georgia, was supplied by Dr. John Bozeman, of Georgia Southern College, who has retained a voucher specimen. *Elliottia paniculata* was obtained from two sources: 1) Dr. G. Murata, Kyoto University, who collected the material from its native habitat; and 2) my garden (B. A. B.). *Elliotia bracteata* was also available from my garden. Voucher specimens have been prepared; living material of the latter two taxa is being maintained.

Extraction and isolation. Dried material was extracted by repeated soaking with 80 percent methanol, usually with three or four changes of solvent; the extracts were pooled. Fresh material was blended with 80 percent methanol at room temperature in a Waring blender. (The material extracted included leaves, stems, and flowers.) The ground mass was filtered and reextracted with 80 percent methanol by letting it stand, with occasional stirring, for two hours. Three or four changes of solvent gave complete extraction as judged by color loss of the leaf material; the extracts were again pooled and evaporated *in vacuo* at 30°. The resulting aqueous suspension was filtered through a bed of Celite Analytical Filter Aid. Any chlorophyll remaining at this stage was removed by shaking a few times with cyclohexane. The aqueous solution was saturated with NaCl and extracted ten times with ethyl acetate in a separatory funnel. In order to be sure that the more polar constituents had been extracted, two extractions with water-saturated n-butanol were performed. The ethyl acetate and n-butanol extracts were compared by two dimensional thin layer chromatography (TLC); in all cases in this study the two extracts were the same and were combined.

Isolation and purification of the flavonoid glycosides were accomplished by the methods described in detail by Wilkins and Bohm (1976). Structural analyses were based upon standard ultraviolet spectrophotometric methods (Mabry *et al.*, 1970). The proton magnetic resonance (PMR) spectrum of quercetin 3-O-arabinoside (determined as the pertrimethylsilyl ether) was obtained using a Varian HA-100 instrument. Tetramethylsilane was used as the internal standard.

Results. Twenty-two flavonol glycosides have been isolated and identified from the four species examined (TABLE 2). The majority of these compounds are derivatives of kaempferol and quercetin, with quercetin being the major aglycone present in all taxa. Three myricetin glycosides

TABLE 2. **Flavonoid distribution in the Cladothamneae.**

	Cladothamnus pyroliflorus	*Elliottia racemosa*	*Elliottia paniculata*	*Elliottia bracteata*
K-3-O-arabinoside	+	+	+	
3-O-glucoside	+	+	+	+
3-O-galactoside	+	+	+	
3-O-gln	+	+	tr	+
3-O-rha	+			
3-O-rutinoside		+	+	+
3-O-gal-7-O-rha	+			
3-O-ara-7-O-rha	+			
Q-3-O-ara	+[a]	+[a]	+[a]	
3-O-glc	+[a]	+	+[a]	+
3-O-gal	+	+	+	
3-O-gln	+	+	tr	+
3-O-rha		+		
3-O-rutinoside		+	+	+
3-O-rha-ara			+	
0-O-gal-7-O-rha	+			
3-O-ara-7-O-rha	+			
7-O-rha	+			
IR-3-O-rutinoside			+	
M-3-O-ara	+	+	+	
3-O-glc	+	+	+	
3-O-gal			+	

Explanation of abbreviations: K = kaempferol; Q = quercetin; IR = isorhamnetin; M = myricetin; ara = arabinose; glc = glucose; gal = galactose; gln = glucuronic acid; rha = rhamnose; a = isomeric pair of glycosides; + = present; tr = trace only; no entry = absence of compound.

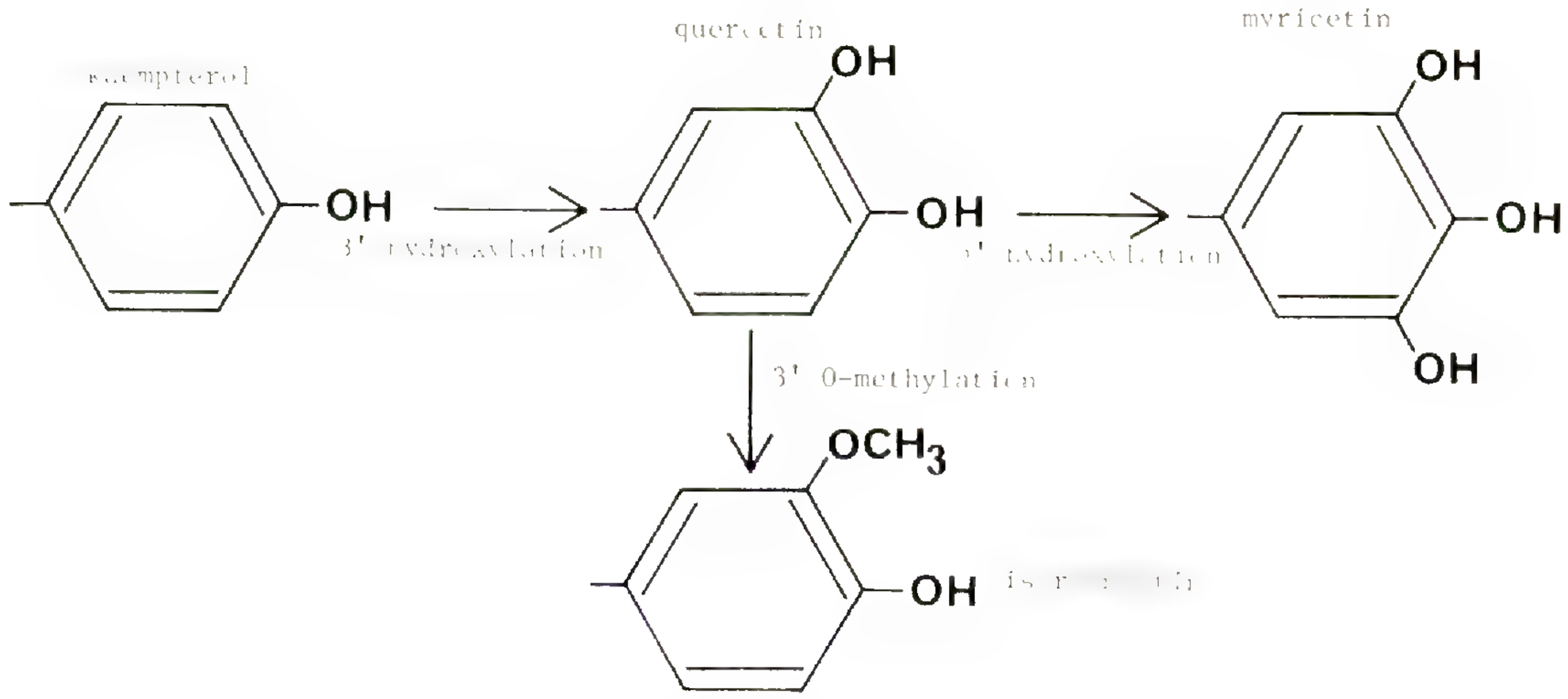
were found. A small amount of isorhamnetin-3-O-rutinoside was found in *Elliottia paniculata*. Within the tribe, *Cladothamnus pyroliflorus* is the only species that makes 3, 7-di-O-glycosides (Bohm & Saleh, 1972). Both kaempferol and quercetin occur as the 3-O-galactosyl-7-O-rhamnosides and 3-O-arabinosyl-7-O-rhamnosides. Reexamination of *C. pyroliflorus* showed a small amount of quercetin-7-O-rhamnoside not noticed before (Bohm & Saleh, 1972).

Three species accumulate pairs of isomeric quercetin-3-O-monosides. *Cladothamnus pyroliflorus* had a pair of quercetin-3-O-arabinosides and a pair of 3-O-glucosides. *Elliottia racemosa* and *E. paniculata* had pairs of 3-O-arabinosides, while *E. paniculata* had a pair of 3-O-glucosides as well. The predominant member of the arabinoside pair from *E. paniculata* was shown to be the β-D-pyranoside by PMR. The predominant member of the glucoside pairs was also the β-D-pyranoside; this was determined on the basis of chromatography against standards known to possess this configuration. In all cases the pyranosides chromatographed more slowly than did the isomeric compounds.

Elliottia paniculata possessed a quercetin-3-O-glycoside derivative that ran in aqueous systems on polyamide plates approximately halfway between the 3-O-glucoside and the 3-O-rutinoside. Total acid hydrolysis yielded quercetin, arabinose, and rhamnose, while partial acid hydrolysis yielded arabinose and a compound indistinguishable from quercetin-3-O-rhamnoside, so the diglycoside is quercetin-3-O-arabinosylrhamnoside. The position of attachment of the "outer" sugar was not determined. Careful search failed to detect this compound in the other taxa.

Discussion. Full use of chemicals for systematic purposes requires knowledge of their biosynthesis and interrelationships. In the case of flavonoids, much is known about the pathways by which the various types are made. Details of some of the steps have been obtained by studying the inheritance of flavonoid pigments and by investigating substrate specificity of enzymes of the pathways. By looking at systems in other plant groups, it is possible to discuss the flavonoid glycoside differences seen in the Cladothamneae in terms of single biochemical steps. Although neither enzymatic nor genetic studies of the Cladothamneae flavonoids have been reported, enough of these other systems is known to suggest that the formation of flavonoids follows much the same route in all plant groups. Some pertinent genetic and enzymatic results are reviewed below.

The formation of the aglycone types found in the Cladothamneae can be summarized by the following abbreviated sequence (flavonol A-rings are omitted for clarity).



It is known that different genes control 3′ and 5′ hydroxylation of anthocyanins as well as flavones and flavonols in several plants (Harborne, 1967). Harborne (1967) also listed several plants in which O-methylation was shown to be controlled by a single gene. Ebel *et al.* (1972) presented evidence showing that specific flavonol O-methyltransferases exist in cultured cells of parsley.

Flavonoid monoglycosides are formed by transfer of the sugar moiety of a nucleoside diphosphate sugar to one of the hydroxyl groups of a flavonoid. Enzymatic and genetic evidence suggest that each such event is under strict control. Using preparations from *Phaseolus vulgaris*, Marsh

(1960) demonstrated the enzymic formation of quercetin 3-O-glucuronide. Similarly, Barber and Chang (1968) showed that an enzyme from *Leucaena glauca* catalyzed the biosynthesis of quercetin 3-O-rhamnoside.

Harborne (1967) has reviewed the genetics of glycosylation reactions in a variety of plants. Typical of the results are the observations of Lawrence and Sturgess (1957) and Harborne (1963) on the inheritance of flower color in *Streptocarpus hybrida*. Separate genes control 3-glycosylation and 5-glycosylation of anthocyanins. Separate genes also control xylosylation to give anthocyanin 3-sambubiosides and rhamnosylation (of 3, 5-diglucosides) to give the 3-rutinoside-5-glucosides. Additional support for the stepwise formation of diglycosides comes from the work of Barber (1962), who showed that the formation of quercetin 3-O-rutinoside occurs in *Phaseolus aureus* by successive enzyme reactions. In recent work with cell cultures of parsley, Sutter and coworkers (Sutter *et al.*, 1972; Sutter & Grisebach, 1973) have shown the existence of two separable glycosylating enzymes with different positional and substrate specificities. Uridine diphosphate glucose (UDP-glucose) : flavone/flavonol 7-O-glucosyltransferase was specific for the 7-position and would not accept 3-O-glycosides as substrates. The second system, UDP-glucose : flavonol 3-O-glucosyltransferase, was specific for the 3-position but would accept flavonol 7-O-glycosides as substrates.

The flavonoid glycosides of the Cladothamneae are based upon the common aglycones kaempferol, quercetin, isorhamnetin, and myricetin (TABLE 2). *Elliottia bracteata* has kaempferol and quercetin glycosides only; *Cladothamnus pyroliflorus* and *E. racemosa* make kaempferol, quercetin, and myricetin glycosides, while *E. paniculata* goes one step further and accumulates the three hydroxy flavonols as well as the O-methylated flavonol isorhamnetin. Thus, on the basis of aglycone elaboration, *E. bracteata* and *E. paniculata* can be distinguished from one another and from the other two taxa, which are indistinguishable.

In the case of monoglycoside composition, *Elliottia bracteata* can be distinguished from the other three taxa by its simplicity, only glucosides and glucuronides being found. The other taxa make both of these, as well as arabinosides and galactosides. *Elliottia racemosa* can be distinguished from the other taxa by its ability to make quercetin 3-O-rhamnoside. *Cladothamnus pyroliflorus* has kaempferol 3-O-rhamnoside and quercetin 7-O-rhamnoside. *Elliottia paniculata* has the capacity to make quercetin 3-O-rhamnoside, but this compound is converted to the 3-O-arabinosylrhamnoside; no monorhamnoside was detected. *Elliottia bracteata* does not make monorhamnosides, but does have the capacity to make rhamnosylglucosides (rutinosides).

Interesting differences exist in the diglycoside fraction of the four species. The three species of *Elliottia* contained 3-O-rutinosides, but *Cladothamnus pyroliflorus* did not. A striking feature of *C. pyroliflorus* is its capacity to make flavonol-3-O-galactoside-7-O-rhamnosides and 3-O-arabinoside-7-O-rhamnosides. It seems reasonable to postulate that this represents a significant difference in rhamnosyltransferase enzymes compared

to the other three members of the tribe. In *Elliottia* rhamnosylation occurs at position 3 of the flavonol or at the 6″ position of the flavonol-3-O-glucosides. *Cladothamnus pyroliflorus* appears to be able to carry out the first of these reactions (it had kaempferol-3-O-rhamnoside), but it does not convert the product further. It can also make the 3-O-glucoside, but further rhamnosylation to the rutinoside does not occur. Finally, *C. pyroliflorus* was found to have quercetin-7-O-rhamnoside, unique in the tribe. In line with the specificity findings of Sutter and coworkers (1972, 1973), this last compound could serve as substrate for enzymes transferring arabinose and galactose to the 3-position of the 7-O-rhamnosides.

One further distinction can be based upon diglycoside data. *Elliottia paniculata* and *E. bracteata* have in common the capacity to synthesize rutinosides, but they can be distinguished from one another on the basis of the formation of quercetin-3-O-arabinosyl-rhamnoside in the former but not in the latter.

GENERAL DISCUSSION

Despite our rather considerable knowledge of the variation in the Cladothamneae, the main points of which are summarized in TABLE 3, the decision as to how many genera should be recognized is still not an easy one. When the Cladothamneae are considered in terms of unique characters or character states that one or more species may have, it is clear that both *Elliottia racemosa* and *Cladothamnus pyroliflorus* are individually more different from the other three species than are *E. bracteata* and *E. paniculata*, although the species pairs *E. bracteata-C. pyroliflorus* and *E. paniculata-E. racemosa* each have a number of characters in common.

Elliottia racemosa differs from all other Cladothamneae in its more or less closed petiole and lamina bundle (and perhaps also in characters of wood anatomy: cf. Cox, 1948), in its inflorescence, which usually lacks a terminal flower, and in its thick-walled capsules with flattened, winged seeds that are shed only tardily. *Cladothamnus pyroliflorus* differs from the other three species in its copper-colored petals, sessile gynoecium, and unvascularized nectary, as well as in several aspects of the flavonoid chemistry (see also TABLE 2). Of the latter, the occurrence of 7-O-rhamnosylation and the associated "diglycoside replacement" is perhaps most important. The species pairs *Elliottia bracteata-Cladothamnus pyroliflorus* and *E. paniculata-E. racemosa* have in common stomatal configuration, calyx size and type, and flower type.

There are numerous other differences in morphology, anatomy, and flavonoid chemistry (aglycone structure and richness and complexity of glycosylation types) that allow the ready recognition of each species and that help to give them their very distinctive individual appearances. These would support the recognition of genera if suggested by other evidence, but of themselves are insufficient to characterize genera. Of greater significance are the numerous characters that all four species have in common, at least some of which might be expected to vary if one were dealing with

Table 3. Variation of some characters among species of the Cladothamneae.

	Elliottia racemosa	Elliottia paniculata	Elliottia bracteata	Cladothamnus pyroliflorus
Two periods of growth per season	-	+(-)	+-	-
Buds with imbricate bud scales	-	++	+	-
Petiole bundle closed or deeply arcuate	+	-	-	-
Stomata without accessory cells	-	-	+	+
Leaves long-petiolate	+	-	-	-
Lamina rounded at the apex, but mucronulate	-	-	+(-)	+
Inflorescences branched	+-	+	-(+)	-
Inflorescences usually with a terminal flower	-(+)	+(-)	+	+
Sepals free, foliaceous	-	-	+	+
Calyx lobe/sepal number	4-5	(3-)5(-6)	(4-)5	5-6
Petal number	4-5	3-4	3	5-6
Corolla basically white	+	+	+	-
Stamen number	8-10	(5-)6-8	5-6	8-10
Gynoecium stipitate	+	++	+	-
Nectary exposed, style curved more than 90°	-	-	+	+
Number of ovules per loculus	8-10	intermediate	numerous	numerous
Capsule thick-walled	+	-	-	-
Seeds strongly flattened and winged	+	-	-	-
Nectary vascularized	+	+	+	-
Myricetin glycosides	+	+	-	+
Isorhamnetin 3-O-rutinoside	-	+	-	-
Monoglycosides - arabinosides and galactosides only	-	-	+	-
Diglycosides - 3-O-rutinosides	+	+	+	-
3, 7-di-O-glycosides	-	-	-	+
Quercetin 7-O-rhamnoside	-	-	-	+

Explanation of symbols: + = present; ++ = present, very strongly developed; - = absent; () = uncommon state.

different genera; these characters are summarized in the tribal description in the introduction. The significance of the characters that typify the three groupings above is much vitiated by the basic similarity of all four species. The similarity in the pollen of the four species is perhaps to be expected in the Ericaceae; see the limited amount of variation found by Oldfield (1959) in his study of some European taxa.

Elliottia racemosa, suggested by Stevens (1971) as being distinct, can be recognized only by its long-petiolate leaves, woody capsules, and flat-

tened seeds. The inflorescence is similar in structure to that of *E. paniculata*, and the difference in leaf anatomy can be used only to support a genus otherwise well founded: the variation in leaf anatomy found in the Cladothamneae as a whole is common at the infrageneric level elsewhere in the Ericaceae (e.g., *Befaria*, *Rhododendron*, and *Kalmia*).

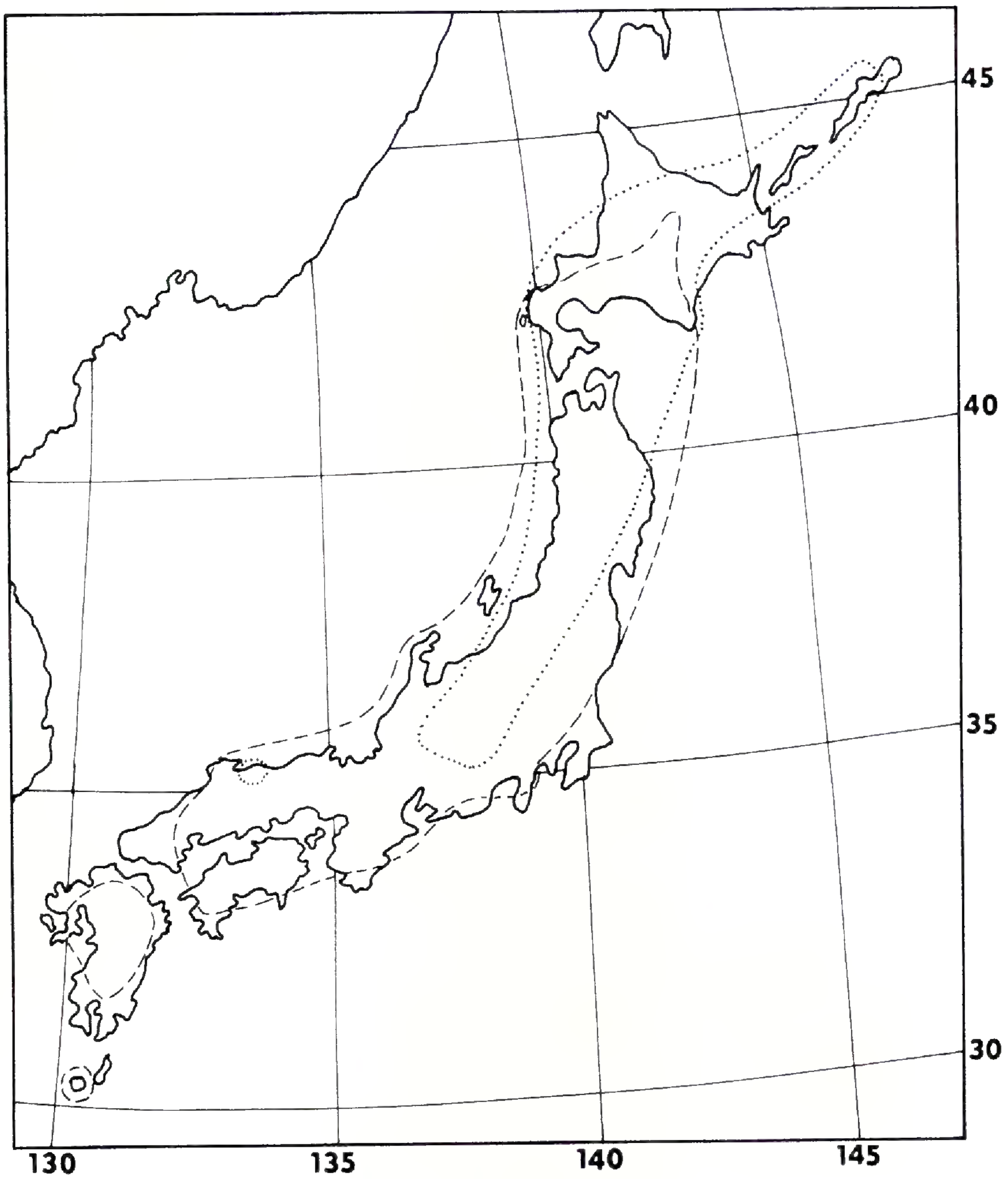
Cladothamnus pyroliflorus is perhaps the most distinctive of the four species in its general appearance. Copeland (1943), following Hooker (1876), distinguished *Cladothamnus* in a key by its sessile leaves that were rounded at the apex, and by its flowers, which were terminal or from the axils of the highest leaves and had 5 or 6 petals (*Elliottia* had petiolate leaves that were acute at the apex, paniculate inflorescences, and flowers often with 3 or 4 petals). It will be clear from TABLE 3 and the preceding discussion that the two latter characters are of little significance; *E. bracteata* has very shortly petiolate leaves that are often broadly rounded and mucronate at the apex and, in these characters, are like leaves of *C. pyroliflorus*. Thus *C. pyroliflorus*, rather like *E. racemosa*, is distinctive mainly because it stands at one end of a number of trends in the Cladothamneae: leaf type, inflorescence elaboration, calyx size, numbers of flower parts. In flower color, sessile gynoecium, and non-vascularized nectary (the last two might be indirectly connected), *C. pyroliflorus* stands somewhat apart from the other Cladothamneae, and it is the only species with a flavonoid chemistry distinctive enough to support generic rank, but the morphological differences are too slight to maintain it as a monotypic genus.

The characters distinguishing *Cladothamnus pyroliflorus* and those distinguishing *Elliottia racemosa* from the rest of the Cladothamneae are rather different. The inflorescence type of *E. racemosa* is clearly derived, and the winged seed also seems to be a specialization of the ellipsoid seed found elsewhere in the Cladothamneae. Flowers in the Ericaceae are basically 5-merous, and the 4-merous flowers of *E. racemosa* with their stipitate gynoecia are probably derived, although less so than those of *E. bracteata* and *E. paniculata*. The closed petiole bundle of *E. racemosa* is possibly less derived than the open condition found in the rest of the genus. In *C. pyroliflorus*, on the other hand, it is possible that only the vegetative characters are derived, and even in these characters *C. pyroliflorus* approaches *E. bracteata*. Unfortunately, not enough is known of the chemical characters to enable discussion concerning whether or not they are derived.

The suggestion that there are two groups in the Cladothamneae, *Elliottia paniculata-E. racemosa* and *E. bracteata-Cladothamnus pyroliflorus*, is a novel one, although Stapf (1934) approached this arrangement when he suggested that his genus *Botryostege* (*E. bracteata*) was closer to *C. pyroliflorus* than to the other two species, which he placed in *Elliottia*. However, it should be remembered that the nectary is protected in different ways in *E. paniculata* (by the bowed filaments) and *E. racemosa* (primarily by the petals). It is also possible that the presence of a large, foliaceous calyx may be functionally correlated with a flat-lying corolla, the large calyx

providing additional support to the platform on which the insects land. In view of the more obvious differences between *E. bracteata* and *C. pyroliflorus*, the recognition of two genera, each with two species, has little to recommend it.

The most satisfactory (or perhaps least unsatisfactory) taxonomic treatment of the Cladothamneae is as a single genus, *Elliottia*, containing four very distinct species that are related in a somewhat reticulate fashion. The names of the species are listed below, and their main synonymy given. Hooker (1876) placed the three species that he included in *Elliottia* (he did not include *Cladothamnus pyroliflorus*) in separate, unnamed sections. Nakai (1922) placed the Japanese species in separate sections with-

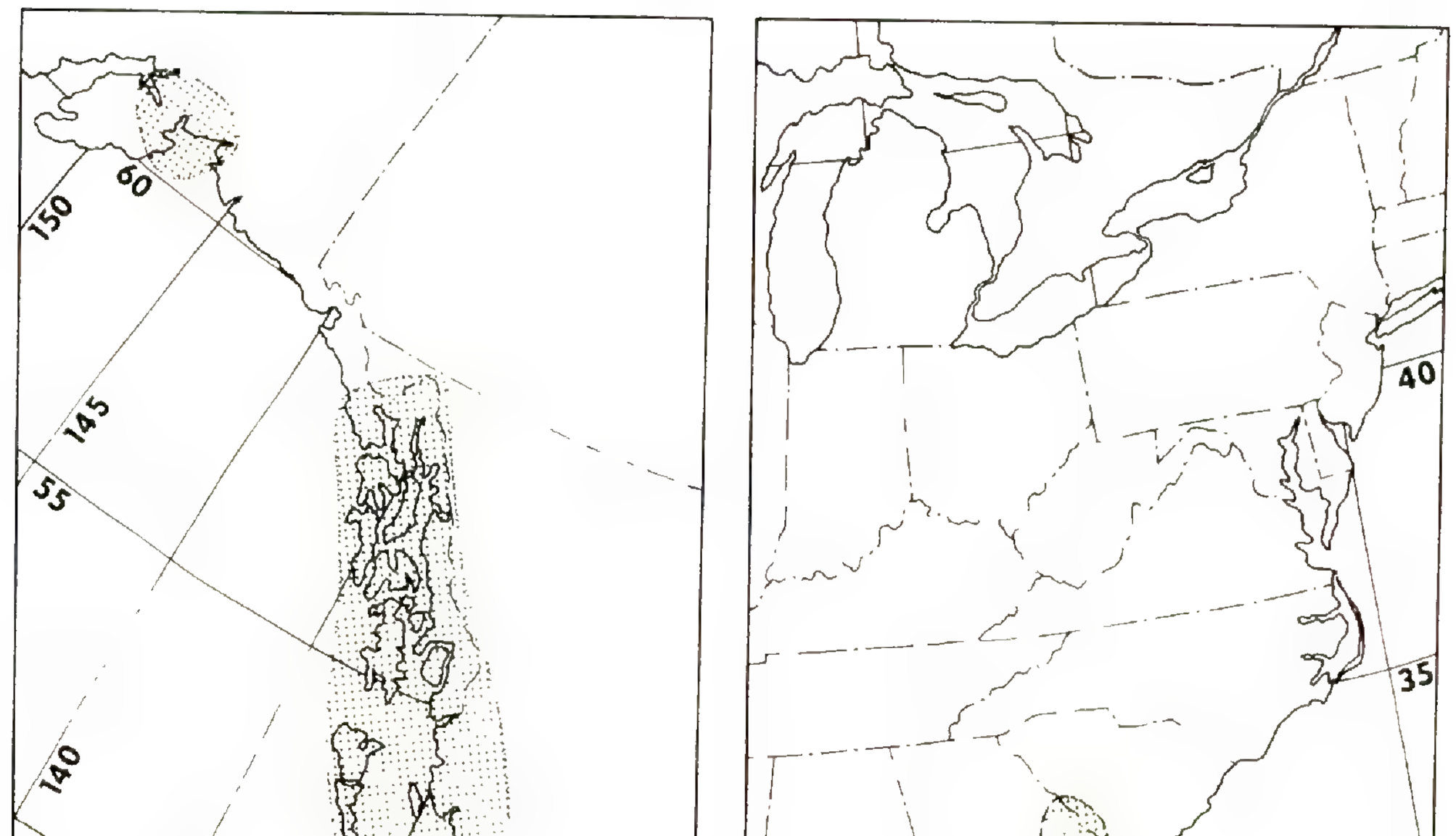


MAP 1. Distribution of *Elliottia* in Japan: dots, *E. bracteata* (from Horikawa, 1972); dashes, *E. paniculata* (from H. Hara, 1958).

in *Tripetaleia*: sect. EUTRIPETALEIA (properly TRIPETALEIA) included *T. paniculata*; sect. SCHIZOCALYX Nakai included *T. bracteata*. The present authors feel that, rather than formally placing each species in a separate section or subgenus, it seems sufficient to remember that all four species are very distinct.

Elliottia as circumscribed here has a disjunct distribution, with *Elliottia bracteata* and *E. paniculata* growing in Japan (MAP 1), *E. pyroliflora* found scattered along the northwest coast of North America from Alaska to Oregon (MAP 2), and *E. racemosa* occurring in the southeastern United States (Georgia and, formerly, South Carolina: MAP 3). This and similar disjunctions (about 50 genera are involved — see Wood, 1972, for references) probably result from the disruption of a widespread early Tertiary flora by climatic change and orogenic events (Graham, 1972).

The four species of *Elliottia* grow in more or less acid and moist habitats, as is common in the Ericaceae. *Elliottia bracteata* grows in grasslands immediately surrounding snowbeds (Ishizuka, 1974) and in mon-



MAPS 2, 3. Distribution of *Elliottia* in North America: 2 (left), *E. pyroliflora* (partly from Hultén, 1968, and Szczawinski, 1962); 3 (right), *E. racemosa*.

tane broadleaf-evergreen forests, and *E. paniculata* grows in similar habitats, but at somewhat lower altitudes. *Elliottia pyroliflora* grows in moist forests, near streams and bogs, along shores, and near the tree line as thickets in openings in hemlock-spruce forests (Calder & Taylor, 1968). *Elliottia racemosa* seems to do best on moist, well-drained sand in mixed woods rather near streams, but it also grows in such habitats as oak-dominated forests, ridges, and *Pinus australis* savannas (Wood, 1961).

Elliottia Muhlenberg ex Elliott, Sketch Bot. South Carolina Georgia 1: 448. 1817.

Cladothamnus Bongard, Mém. Acad. Sci. St.-Pétersb. Sci. Nat. VI. 2: 155. 1832.
Tolmeia Hooker, Fl. Bor.-Am. 2: 44. 1834.
Tripetaleia Siebold & Zuccarini, Abh. Bayer. Akad. Math. Phys. Kl. 3: 731. 1843.
Botryostege Stapf, Kew Bull. **1934:** 194. 1934.

Key to the Species of Elliottia

1. Inflorescences usually with fewer than 4 flowers; sepals ca. 15 mm. long; petals copper colored; ovary sessile. . . . . 3. *E. pyroliflora.*
1. Inflorescences nearly always with more than 3 flowers; sepals at most ca. 5 mm. long; petals white, tinged with red; ovary stipitate.
   2. Lamina often ± rounded at the apex, mucronate; calyx of free sepals ca. 5 mm. long; nectary exposed in open flower. . . . . 1. *E. bracteata.*
   2. Lamina cuneate to acute at the apex, whether or not mucronate; calyx connate, less than 2 mm. long; nectary concealed in open flower.
      3. Twigs subterete; petiole 0.3–1.8 cm. long; capsule woody; seeds flattened. . . . . 4. *E. racemosa.*
      3. Twigs strongly angled; petiole less than 4 mm. long; capsule not woody; seeds not flattened. . . . . 2. *E. paniculata.*

1. **Elliottia bracteata** (Maximowicz) Hooker f. in Bentham & Hooker f. Gen. Pl. 2: 598. 1876; *Tripetaleia bracteata* Maximowicz, Bull. Acad. Sci. St.-Pétersb. III. 11: 432. 1876; *Botryostege bracteata* (Maximowicz) Stapf, Kew Bull. **1934:** 194. 1934. Syntypes: Japan. Yeso [near Hakodate], variis locis, *Maximowicz*; Nambu, 1865, *Tschonoski.*

1a. **Elliottia bracteata** (Maximowicz) Hooker f. forma **bracteata.**

1b. **Elliottia bracteata** (Maximowicz) Hooker f. forma **longiracemosa** (Nakai) Brim & P. F. Stevens, comb. nov.

Tripetaleia bracteata Maximowicz var. *longeracemosa* Nakai, Bot. Mag. Tokyo **44:** 530. 1930; *Botryostege bracteata* (Maximowicz) Stapf forma *longeracemosa* (Nakai) Hara, Bot. Mag. Tokyo **50:** 562. 1936. Type: Japan. Yeso, in monte Apoi, prov. Hidaka, *T. Nakai.*

2. **Elliottia paniculata** (Siebold & Zuccarini) Hooker f. in Bentham & Hooker f. Gen. Pl. 2: 598. 1876; *Tripetaleia paniculata* Siebold &

Zuccarini, Abh. Bayer. Akad. Math.-Phys. Kl. 3: 732. 1843. TYPE: Japan, *Siebold*.

T. yakusimensis Nakai, Bot. Mag. Tokyo 40: 485. 1926. TYPE: Japan. Yakushima, in monte Yaedake, *Kimura*.

3. **Elliottia pyroliflora** (Bongard) Brim & P. F. Stevens, comb. nov.

Cladothamnus pyrolaeflorus Bongard, Mém. Acad. Sci. St.-Pétersb. Sci. Nat. VI. 2: 155. 1832; *Leiophyllum pyrolaeflorum* (Bongard) Dippel, Handb. Laubholzk. 1: 436. 1889. TYPE: [Alaska.] New Archangel, *Mertens*.

Pyrola fruticosa Esch. ex Ledebour, Fl. Ross. 2: 924. 1824. Nomen.[2]

Tolmeia occidentalis Hooker, Fl. Bor.-Am. 2: 44. 1834. TYPE: northwest coast of America, *Menzies*.

4. **Elliottia racemosa** Muhlenberg ex Elliott, Sketch Bot. South Carolina Georgia 1: 448. 1817. SYNTYPES: Georgia. Waynesborough, Burke County, *anon.*; Oconee, *Jackson*.

The reassessment of the generic limits in the Cladothamneae raises some points of more general importance in considering the evolution of the Ericaceae as a whole. *Befaria*, with its terminal inflorescences and polypetalous flowers with large and variable numbers of parts, has often explicitly or implicitly been considered to be the most primitive member of the Rhododendroideae and/or the Ericaceae as a whole (Copeland, 1943, and references; N. Hara, 1958), and the Cladothamneae have been placed close to the Befarieae. Reevaluation of the available evidence shows that there is no necessity to consider *Befaria* and *Elliottia* to be more closely related to each other than to any other Rhododendroideae, and that it is very difficult to assess the position of either genus in any phyletic system of the family.

Although Stebbins (1974, p. 267) cites the Ericaceae as a family in which all members have indeterminate (racemose, polytelic) inflorescences, this is clearly not so; however, monotelic inflorescences seem to be uncommon outside the Cladothamneae. *Befaria racemosa* Vent. (Rhododendroideae - Befarieae) very occasionally has three-flowered branches with a terminal flower, the inflorescence having a structure similar to that shown in FIGURE 1, F (*R. & M. Kral 6715*). In *Ledothamnus* Meissner (Rhododendroideae - Phyllodoceae) there are reports of terminal inflorescences and sometimes single flowers (e.g., Copeland, 1943), but the flowers in the inflorescences examined were all axillary; careful observation is necessary to confirm that the single flowers are truly terminal. In the Vaccinioideae - Andromedeae, *Craibiodendron* W. W. Sm. has flowers apparently terminating the main axes (although these are usually broken off in herbarium specimens) and certainly terminating the lateral axes of

[2] Baillon (Adansonia 1: 197. 1860) described a plant from "California" that Douglas called *Pyrola fruticosa*. Although Baillon clearly considered *P. fruticosa* to be a species of *Cladothamnus*, he did not make the combination of *P. fruticosa* under *Cladothamnus*.

the axillary inflorescences. Occasional terminal flowers occur in *Agarista* D. Don (W. Judd, pers. comm.). Terminal flowers are also reported from the Monotropoideae (Copeland, 1941).

There seems to be a consensus that the cymose, monotelic inflorescence is a more generalized (primitive) type than the racemose, polytelic inflorescence. Although there is some discussion as to whether a single, terminal flower or a three-flowered dichasium is the least specialized inflorescence type of all (see Rickett, 1944; Stebbins, 1974), the few-flowered, highly foliated inflorescence of *Elliottia pyroliflora* (FIGURE 1, A) is either the least specialized type (Rickett, 1944) or very close to it, and can be considered the least specialized type in the Ericaceae as a whole.

The inflorescences are also rather unspecialized in the rest of the genus, but there is apparently a transition to the polytelic inflorescence common in the rest of the family, with a concomitant reduction in foliation, increase in number of flowers, and increase in the regularity of insertion of the highest order bracts (the "bracteoles" of the rest of the family). It is relatively easy to derive at least the great majority of inflorescence types in the Ericaceae from those found in *Elliottia*. The inflorescences of *Befaria* are of a derived type, being usually more compact, less foliated, and apparently almost entirely polytelic; the single exception is noted above.

Much of the other evidence as to the primitiveness of *Befaria* and its close relationship with the Cladothamneae is unsatisfactory. Copeland himself noted (1943) that the extremities of the carpels were more perfectly fused in *Befaria* than in the Cladothamneae, although the vascular bundles supplying the various organs of the flower in *B. racemosa* were all separate (this was not so in the Cladothamneae). There seems to be no reason to consider the reduction of the chalazal haustoria of the embryo in the Cladothamneae to be derived rather than the converse. Copeland considered that the presence of resorption tissue in the anthers and of filaments (viscin threads) in the pollen was evidence of the relationship of *Befaria* and the Cladothamneae, since he thought that such a combination of characters did not occur elsewhere in the Rhododendroideae. However, such a combination also occurs in the Phyllodoceae (Stevens, 1971); the mechanism of anther dehiscence in the Epigeaeae and Diplarcheae is unknown. The presence of an endothecium in the anther of *Befaria* (but not in *Elliottia*) may be an unspecialized character. Although *Befaria* may have more than the 5 sepals, petals, and carpels, and the 10 stamens that are common in the Ericaceae, together with infraspecific variation in the numbers of these organs, this again cannot be considered *a priori* a primitive character; such a combination is a derived state in *Rhododendron* section VIREYA, and species of *Lyonia* that have more than the normal number of floral parts are also derived (W. Judd, pers. comm.). *Elliottia pyroliflora* perhaps has comparable variation in the number of floral organs, although in *Elliottia* as a whole there also seems to be a reduction trend toward trimery, culminating in *Elliottia bracteata*. There are good indications that polypetaly may be a derived character in some Ericaceae (*Ledum*, *Vaccinium* L., and the Pyroloideae: Copeland, 1947; Leins,

1964); the transition from polypetaly to sympetaly in the Ericaceae is clearly neither difficult nor indicative of major phylogenetic differences. Finally, Cox (1948) noted that the wood anatomy of *Befaria* was not notably primitive, and, although he thought that it was rather different from the other Rhododendroideae examined, the evidence given hardly supported such a view.

There are several other differences between the Befarieae and Cladothamneae (Stevens, 1971). *Befaria*, so far as has been examined, has perhaps primitive trilacunar nodes (apparently not constantly so in *B. racemosa*) and tetracytic stomata that are oriented more or less at right angles to the long axis of the leaf; *Elliottia* has unilacunar nodes and anomocytic or paracytic stomata that show no particular orientation. The two differ in leaf vernation, *Befaria* having revolute leaves, *Elliottia* convolute. The entire absence of other than unicellular hairs in *Elliottia* is unusual for the Ericaceae and is perhaps a derived character; *Befaria* has multicellular hairs as well. The testa of *Befaria*, with its elongated, thin-walled cells and very fine pitting, is similar to that of most of the Rhodoreae and some of the Phyllodoceae; that of *Elliottia*, with its broadly pitted, polygonal cells, is unique in the Rhododendroideae. Recent evidence on the distribution of phenolics is also interesting (Harborne & Williams, 1973). The two species of Cladothamneae that they studied were distinct from the other Rhododendroideae in lacking all six phenolic constituents characteristic of that subfamily; *Befaria* was readily characterized by the absence of gossypetin and the predominance of 3, 5-O-methyl flavonols and dihydroflavonols. Harborne and Williams (1973) did not find kaempferol in *Befaria*, although it occurs in all the Cladothamneae.

It is clear that we do not have enough knowledge to talk very constructively about relative advancement in the Rhododendroideae. However, *Befaria* and *Elliottia*, both isolated genera, are clearly not close to one another since they have in common no characters that necessarily suggest immediate relationship. *Befaria* is in some ways (phenolics, inflorescence, indumentum, testa) closer to other Rhododendroideae than is *Elliottia*. Each genus appears to have some "primitive" characters, but the final position of the two genera in any phyletic scheme must take into account both the findings on inflorescence types and those on polypetaly; indeed, all characters must be treated much more critically.

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LUMNITZERA ROSEA (COMBRETACEAE) — ITS STATUS AND FLORAL MORPHOLOGY

P. B. TOMLINSON, J. S. BUNT, R. B. PRIMACK, AND N. C. DUKE

THREE FORMS of *Lumnitzera* (Combretaceae) are known to us in Queensland. Two are clearly the common and widespread mangrove species *L. littorea*, with scarlet flowers, and *L. racemosa*, with white flowers. The third form is intermediate (e.g., it has pink flowers) and is very local in distribution. The identity of this third form is the substance of this paper and is set against the background of a description of floral morphology and pollination biology in the genus. In order to name this pink-flowered form, we have to go back to the botanical information that resulted from the French expedition to the South Pacific (1817–20) under the command of Freycinet in the "Uranie" and "Physicienne" (Gaudichaud-Beaupré, 1826–30). The following account is an attempt to link observations made recently in Queensland (FIGURE 1) with the older literature, and to interpret some of the illustrations and names provided by Gaudichaud.

The genus *Lumnitzera* is a common mangrove constituent of the Asian tropics, ranging from Ceylon to Fiji. From existing accounts, its taxonomy and nomenclature would appear to be well stabilized, although based primarily on a study of herbarium specimens (Merrill, 1909; van Slooten, 1924; Exell, 1954). Exell's treatment recognizes two clearly contrasted species, which can be separated as follows:

a. Flowers red, shortly pedicellate; stamens twice as long as petals; inflorescences terminal. ..... *L. littorea* (Jack) Voigt.
b. Flowers white, sessile; stamens equaling or only slightly exceeding the petals; inflorescences axillary. ..... *L. racemosa* Willd.

In addition, there may be differences in the anatomy of the floral cup (hypanthium) and fruit, but we have not examined these in detail.

Exell suggests in his description that *Lumnitzera racemosa* lacks pneumatophores and so differs from *L. littorea*, but in our experience *L. racemosa* can develop the characteristic looped aerial roots (pneumatophores) that are more common in *L. littorea*, the form and degree of development probably varying somewhat in individual trees depending on edaphic conditions.

The two species are not readily distinguishable in the vegetative state since they have similar leaf sizes and shapes. *Lumnitzera littorea* has a more diffuse, sprawling habit with a tendency for lower branches to take root. Variability is, however, illustrated by populations of the same species at Jacky Jacky Creek, Cape York Peninsula (FIGURE 1), which form an upper canopy of trees up to 30 meters high and 65 cm. d.b.h.

The range of the two species in Malesia, as mapped by van Slooten (1924) and more completely by Exell (1954), is very similar. Van Slooten

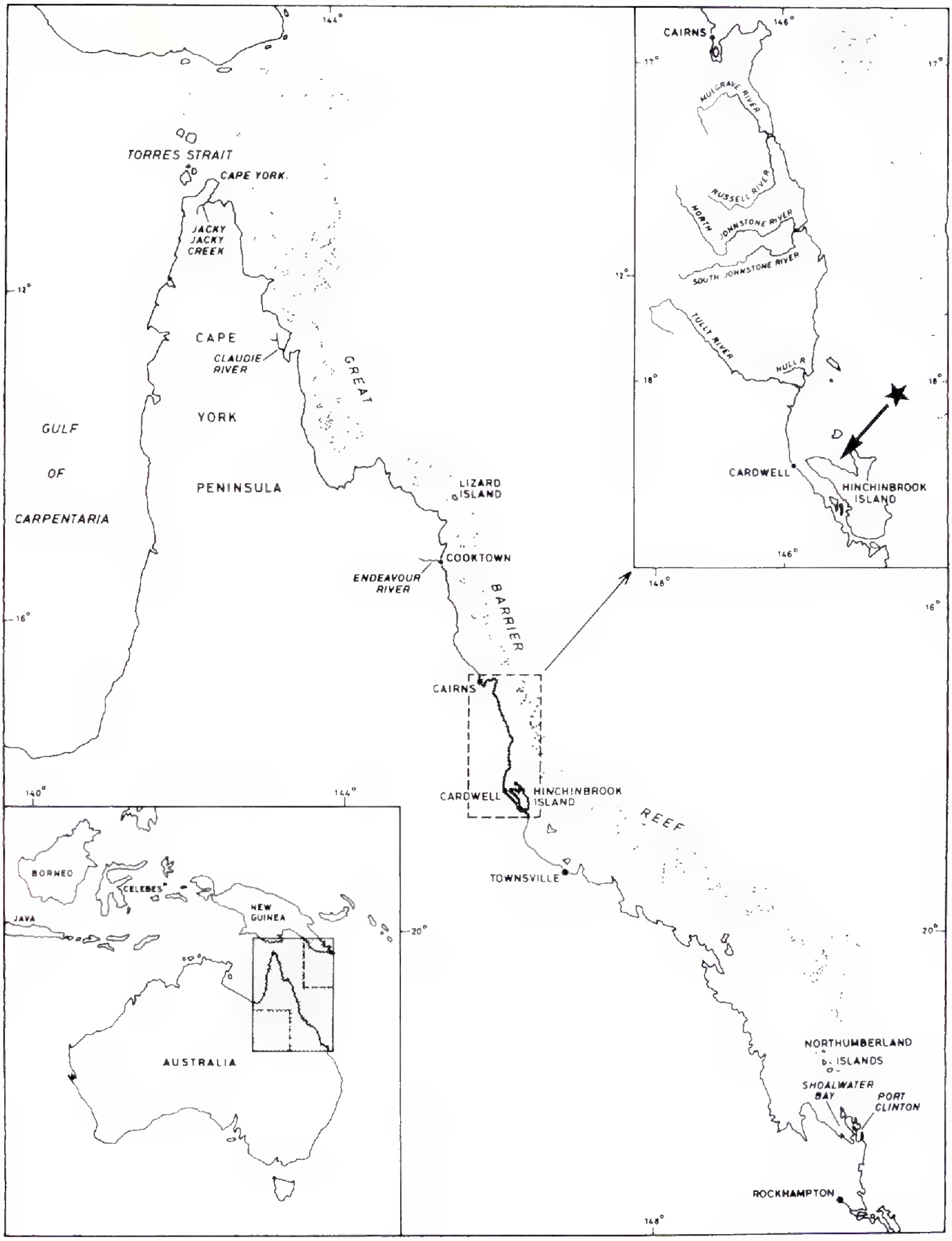


FIGURE 1. Northern Queensland. Inset figures show (lower left) the generalized region and (upper right) the Cairns-Hinchinbrook region in which the most detailed ground observations have been made. *Lumnitzera littorea* and *L. racemosa* occur throughout the generalized region; *L.* × *rosea* occurs only in Missionary Bay, Hinchinbrook Island (arrow).

suggests that they occupy different ecological sites and so exclude each other, but does not give precise details. Our own observations confirm that stands in northern Queensland, almost without exception, contain one species to the exclusion of the other. Further, we have never encountered sequential zones of the two species. Both are confined to the in-

ner mangrove fringe, to the banks of tidal creeks, and, on occasion, to the upper parts of sandy beaches. Their separate distribution in some instances may be a matter of chance. However, it is also likely that each species has unique tolerances that permit separate establishment under conditions that appear very similar only under casual observation. For example, we have often found *Lumnitzera racemosa* but not *L. littorea* growing successfully in association with *Ceriops* and *Avicennia* in the inner mangrove. Equally, it is normally *L. racemosa* that one encounters under the harsh conditions at the margins of bare salt pans. *Lumnitzera littorea* appears better suited to less saline, well-drained sites. Our observations suggest that within such conditions this species develops most vigorously in more highly organic substrates and assumes its well-known shrubby appearance on substrates that might be termed skeletal. A more careful analysis of distribution patterns and associated edaphic conditions will be needed to refine these preliminary impressions.

NOMENCLATURE

A number of other names exist, including *Lumnitzera lutea* (Gaud.) Presl (= *L. racemosa* var. *lutea* (Gaud.) Exell), which was applied to a plant with yellow, axillary flowers, and stamens longer than the petals, described by Gaudichaud-Beaupré as having gland-bearing calyx tips. Originally described from Timor and for a long time known only from Gaudichaud-Beaupré's description, this plant has been more recently collected by Bouman-Houtman (see van Steenis-Kruseman, 1950, p. 187). This is treated by Exell (1954) as a variety of *L. racemosa*, which may be appropriate since gland-tipped calyx lobes occur in both varieties.

All other names but one have even less validity in morphological terms and have been accepted as being based on minor variants of either *Lumnitzera littorea* or *L. racemosa* (van Slooten, 1924; Exell, 1954). The exception is *Lumnitzera rosea* (Gaud.) Presl: we believe that we have rediscovered this entity and can account for its existence.

Gaudichaud-Beaupré (1826) included names now referable to *Lumnitzera* under *Laguncularia*, the appropriate combinations being made by Presl (1834). Of the four names, *Laguncularia lutea* is now considered to be a variety of *Lumnitzera racemosa* (see above), and *Laguncularia coccinea* is a synonym of *Lumnitzera littorea*. *Laguncularia purpurea* is a name used, apparently in error, by Gaudichaud-Beaupré in the plate and legend of the entity that he called *L. coccinea*. *Laguncularia rosea*, described from a specimen collected from Manila, in the Philippine Islands, has subsequently been considered to be a mere color form of *Lumnitzera racemosa*. However, the information given in the diagnosis and the plate allows the three entities to be contrasted clearly (currently accepted nomenclature is used):

Lumnitzera littorea (as *Laguncularia coccinea* and *L. purpurea*) — inflorescence a terminal, elongated spike, flowers "purple," calyx lobes without glands, anthers with or without an appendage.

Lumnitzera racemosa (as *Laguncularia lutea*) — inflorescences axillary, flowers yellow, calyx lobes uniglandular, anthers with an appendage.
Lumnitzera rosea (as *Laguncularia rosea*) — inflorescence axillary, flowers roseate, calyx lobes triglandular, anthers with an appendage.

We will return to these diagnoses after we have considered floral morphology.

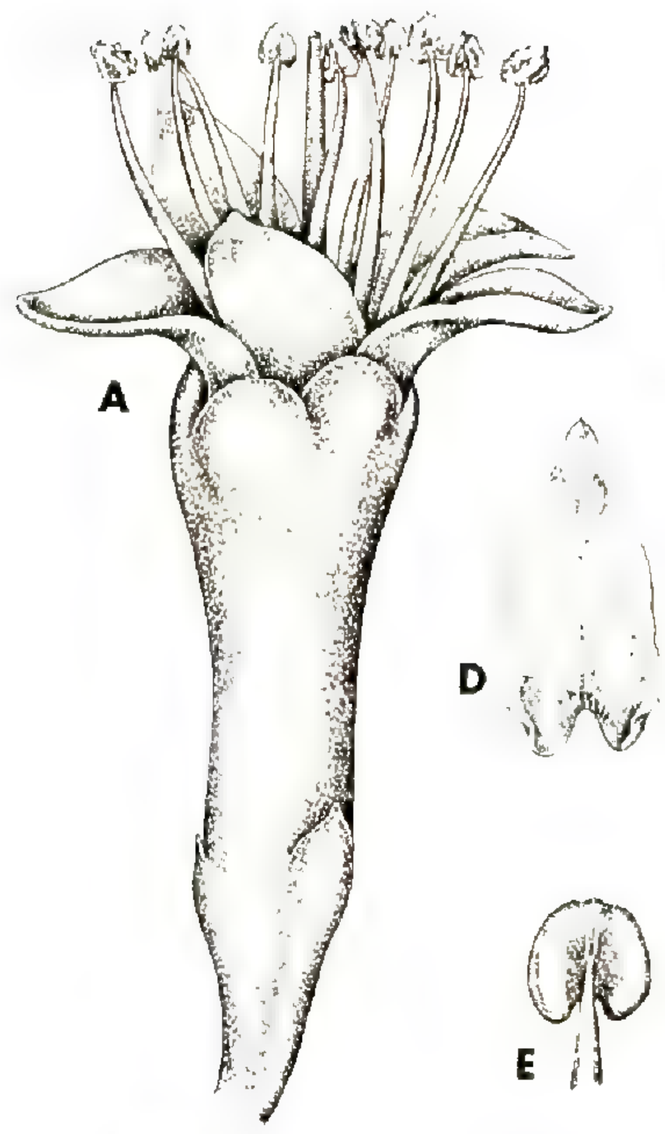
Subsequent authors have used additional diagnostic characters (e.g., stamen number, as suggested by Gagnepain, 1920) in segregating *Lumnitzera littorea* from *L. racemosa*, but they are neither useful nor consistent. Despite this, the most consistently diagnostic floral feature, that of slight zygomorphy versus actinomorphy, has been overlooked by all authors with the exception of Brandis (1893), who illustrated it clearly. Exell (1954) refers to actinomorphic flowers in his generic description of *Lumnitzera*, implying that all species are alike in this respect.

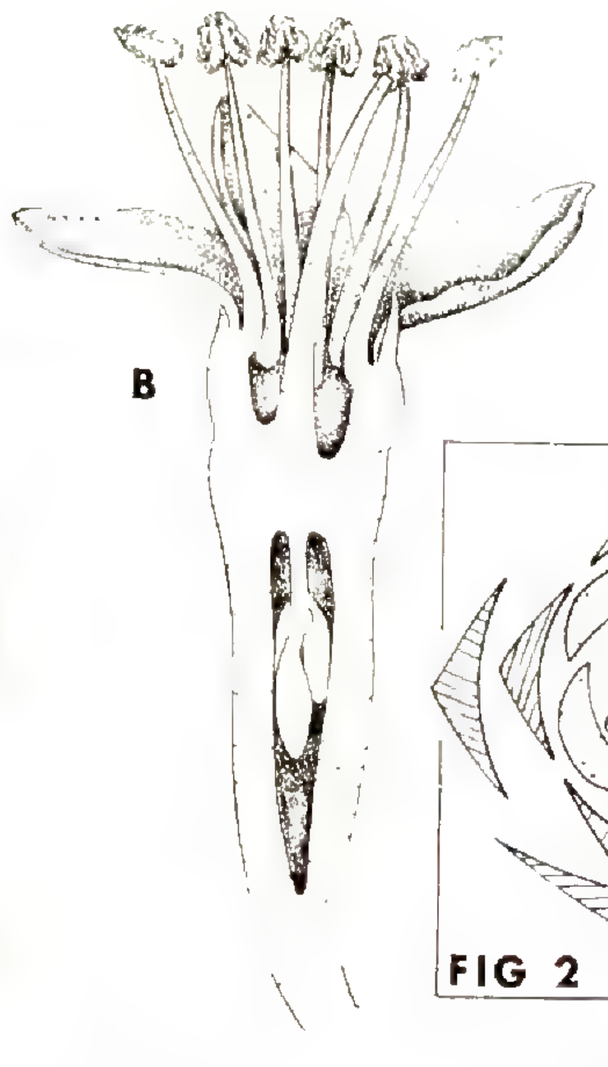
OBSERVATIONS

Floral morphology. Floral features common to *Lumnitzera littorea* and *L. racemosa* are represented diagrammatically in Figure 2. Stamen number is variable, since members of either antesepalous or antepetalous whorls may be missing. Flowers of *L. littorea* (Missionary Bay, Hinchinbrook Island, Queensland, 18°15′ S, 146°15′ E) are illustrated in Figure 4. This shows the short, more or less erect petals, exceeded in length by the erect stamens. Appreciable zygomorphy is shown in the median longitudinal section of Figure 4, B: the calyx tube is oblique, with the style inserted high on one side. This creates a deep tube on the adaxial side of the flower in which abundant nectar, secreted by the inner surface of the tube, accumulates. Zygomorphy is also evident in the slight dorsiventral curvature of the flowers, such that the flower bends upward toward the apex of the spike. The nonmedian position of the style is further shown in the longitudinal section in the plane of insertion of the bracteoles (Figure 4, C). The stamens are unappendaged in this collection (Figure 4, E), although Brandis (1883) does show a stamen appendage in his illustration of this species. Other collections elsewhere in Queensland show that the stamen appendage is an inconstant character.[1] Petals have a broad insertion (Figures 4, D; 6, A, B).

Flowers in *Lumnitzera racemosa* (Figure 5) are strictly actinomorphic; the petals are spreading at maturity and are scarcely exceeded by the somewhat spreading stamens. The calyx tube is shallow and symmetrical; the style is inserted in the center so that it is sectioned equally in both dorsiventral and lateral planes (cf. Figure 5, B, C). Flowers of *L. racemosa* are appreciably shorter than those of *L. littorea*, the relative lengths (including calyx tube and pedicel) being about 18 vs. 8 mm., respectively.

[1] The anther is dorsifixed, but the filament is bent over in bud so that the appendage projects upward. When the filament straightens at anthesis, this orientation is more or less reversed.





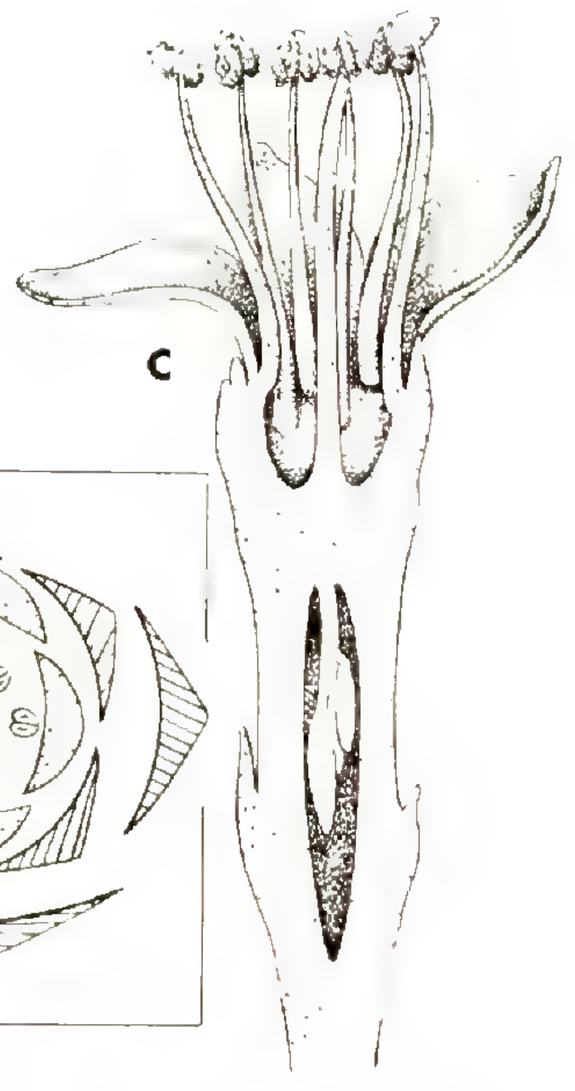


FIG 2

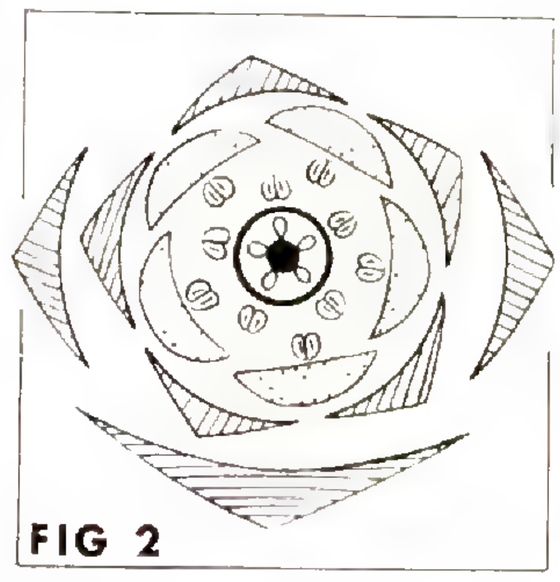
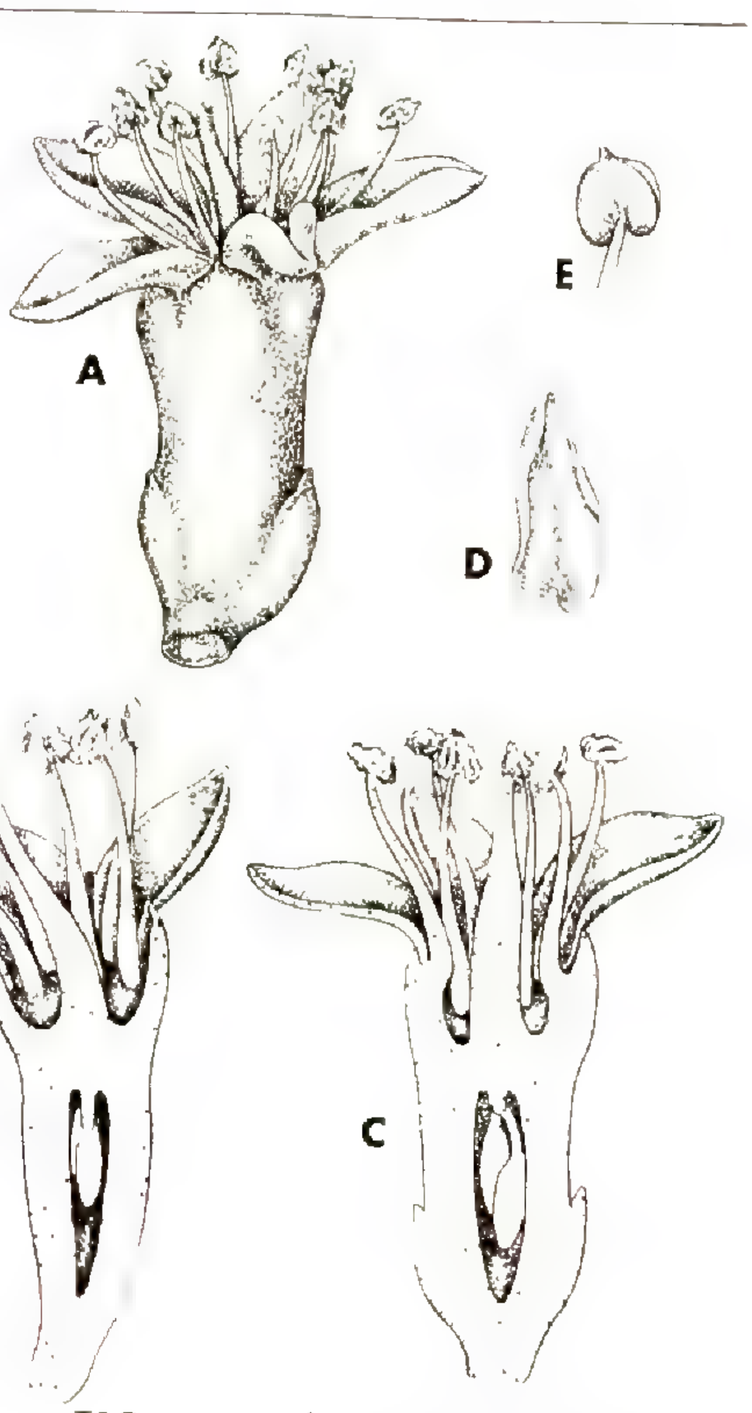


FIG 3 x rosea

FIG 4 littorea



PF FIG 5 racemosa

FIGURES 2–5. Floral morphology in *Lumnitzera*. 2, generalized floral diagram. 3, *Lumnitzera* × *rosea* (Hinchinbrook Island, Queensland): a, flower, side view; b, flower sectioned longitudinally in dorsiventral plane; c, flower sectioned longitudinally in transverse plane; d, petal; e, detail of single anther. 4, *Lumnitzera littorea* (Hinchinbrook Island, Queensland): a, flower, side view; b, flower sectioned longitudinally in dorsiventral plane; c, flower sectioned longitudinally in transverse plane; d, petal; e, detail of single unappendaged anther. 5, *Lumnitzera racemosa* (Hinchinbrook Island, Queensland): a, flower, side view; b, flower sectioned longitudinally in dorsiventral plane; c, flower sectioned longitudinally in transverse plane; d, petal; e, single appendaged anther. Magnifications for figures 3–5: a–d, × 2.5; e, × 6.

The stamens have a distinct connective appendage (FIGURE 5, E), and the petals have a narrow insertion (FIGURE 5, D; 6, D, E).

In both species there is a variable number of anatropous ovules (from 3 to 7, with 5 the most frequent number) suspended from a slender placenta which itself hangs from the upper part of the ovary loculus, as shown in all illustrations of longitudinal sections of flowers in FIGURES 3–5. The ovules are narrow with the micropyle projecting apically.

POLLINATION BIOLOGY. Differences between the species in floral morphology and biology relate to differing methods of pollination. *Lumnitzera littorea* is pollinated predominantly by honeyeaters (Meliphagidae) such as the graceful honeyeater (*Meliphaga gracilis*), as well as by native bees and wasps. Bird pollination is indicated in this species by the red flower color and the abundant nectar that accumulates to one side of the calyx tube. The flowers are longer and the petals are directed forward, orienting the bill of the bird and protecting the nectar from most insects. The stamens are directed forward to touch the bill of the bird. The terminal inflorescences accommodate large pollinators.

Lumnitzera racemosa is frequently visited by a variety of day-active insects such as wasps, solitary and social bees, butterflies, and day-active moths. Wasps, the most common flower visitors observed, aggressively chased the other flower-visiting insects. No insects were observed on the flowers at night. Characters related to pollination by generalized flower-visiting insects are the white flower color and the small amounts of nectar secreted into the shallow calyx tube. The stamens are directed to the side to contact insects that have landed on the reflexed petals. The axillary flowers accommodate small pollinators. Pollen is present in the anthers only on the day the flower opens, while the stigma appears to become receptive on the second and subsequent days.[2] As a result of this marked protandry, individual flowers are probably not capable of self-pollination. Fruit-set is high, probably over 50 percent in many trees, and even on isolated individuals, suggesting that the species is self-compatible.

In Queensland, flowering times differ somewhat in the two species, but there is appreciable overlap: *Lumnitzera littorea* flowers from August, when insects are not yet active, to December; *L. racemosa* from October to March.

LUMNITZERA IN QUEENSLAND. In addition to the two common species of *Lumnitzera* in Queensland, which form a characteristic element of the back mangroves, populations of a pink-flowered form have been located at Missionary Bay on Hinchinbrook Island (FIGURE 1). The inflorescences are terminal, but the flowers are sufficiently distinct to make it difficult to equate this form with *L. littorea*. This population occurs as a pocket in the stand of *L. littorea* that supplied the material for FIGURE 4.

As shown in FIGURES 3 and 6, flowers of this form approach the size of

[2] On the basis of a positive test for esterase activity with α-naphthyl acetate (Heslop-Harrison *et al.*, 1975).

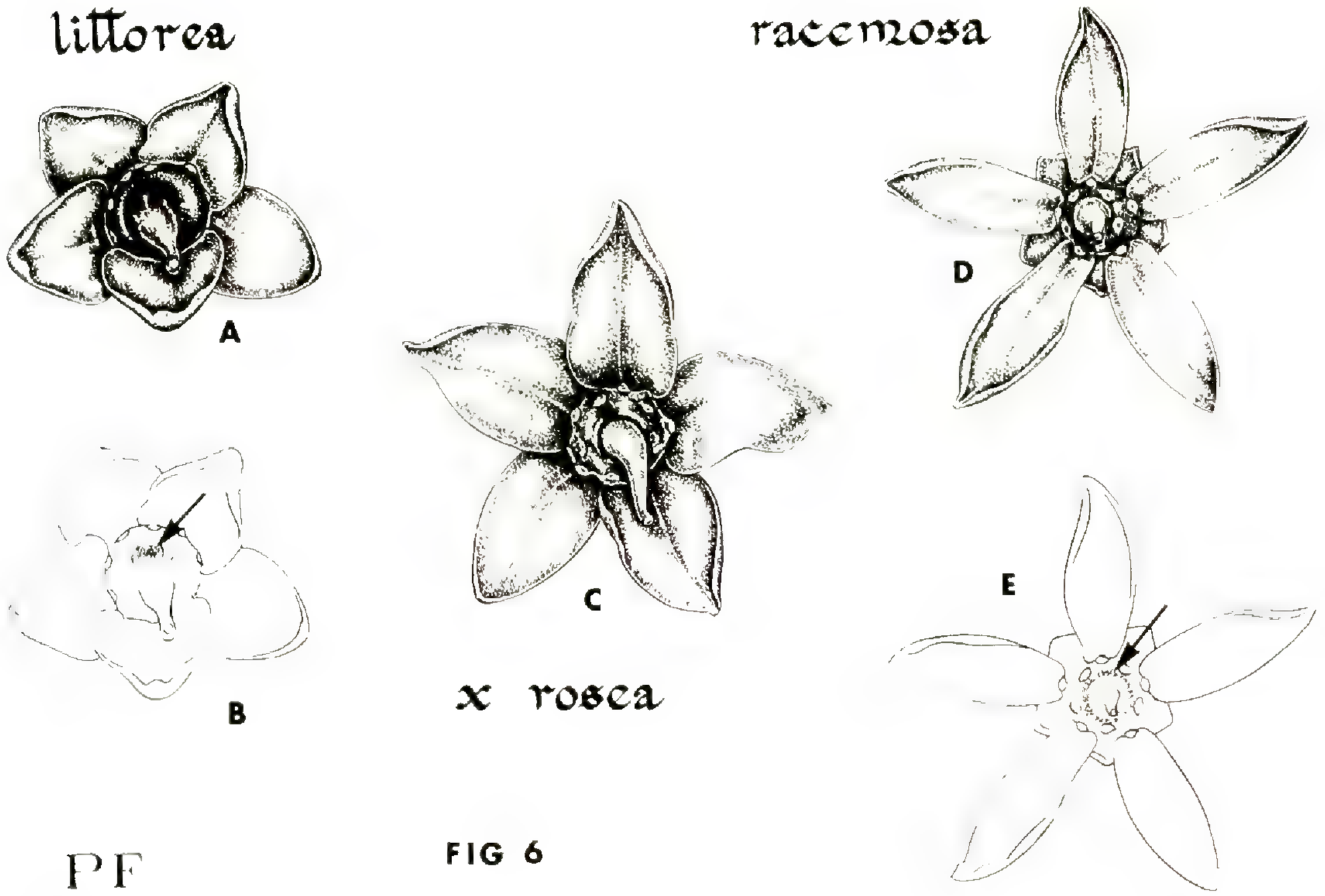


FIG 6

FIGURE 6. Flowers from above (stamens removed), showing petal shape and nectary (arrow) in relation to style: a, b, *L. littorea*; c, *L.* × *rosea*; d, e, *L. racemosa*; all × 2.5.

those of *Lumnitzera littorea*, but are distinguished by the spreading, pink petals. In addition, they are scarcely zygomorphic; although the style is slightly to one side of the calyx tube (FIGURE 3, B), it is still cut when the flower is sectioned in both dorsiventral and lateral planes (FIGURE 3, C). The stamens are shorter than in *L. littorea* and usually have a minute connective appendage, much less prominent than in *L. racemosa* (FIGURE 3, E). The petals have a broad insertion (FIGURE 3, D). Nectar-feeding birds, bees, and wasps have been observed visiting the flowers of this species.

In order to provide an identity for this species, we have adopted the name *Lumnitzera* × *rosea* Gaud., pro sp., making the assumption that the taxon Gaudichaud-Beaupré illustrated corresponds to the form we ourselves have more recently discovered. We provide evidence that the form is a hybrid, *L. littorea* × *racemosa*. This is a considerable assumption, first because *L.* × *rosea* probably originated in the Philippines, and second because Gaudichaud-Beaupré illustrated and described a plant with axillary inflorescences. Third, the type locality for *L.* × *rosea* is believed to be Manila Bay, but, of the two putative parents, only *L. racemosa* has been collected here. However, using this name, we can summarize our field observations of *Lumnitzera* in Queensland in TABLE 1.

We have found, as did Exell, that the number of sepal glands is not very constant and does not provide a reliable means of distinguishing *Lumnitzera* species. In addition, *Lumnitzera* × *rosea* is closer to *L. racemosa* in

TABLE 1. **Floral features of Lumnitzera species in Queensland.**

CHARACTER	SPECIES		
	littorea	× *rosea*	*racemosa*
Inflorescence	terminal	terminal	axillary
Petal color	scarlet	pink	white
Flower length (from insertion to style tip)	16–18 mm.	13–14 mm.	7–8 mm.
Petal position	± erect	± reflexed	± reflexed
Symmetry	slightly zygomorphic	almost actinomorphic	strictly actinomorphic
Stamen appendage	sometimes absent	minute	present
Flower visitors	birds, insects	birds, insects	insects

its more nearly sessile flowers and in the anatomy of the floral cup since it has few rather than many vascular bundles in the cortical region. It resembles *L. littorea* more in its early flowering time, but *L. racemosa* most in habit. However, natural layering of branches occurs as it does in *L. littorea*.

STATUS OF LUMNITZERA × ROSEA. The intermediate status of this pink-flowered form strongly suggests its hybrid origin. This is further supported by pollen sterility of about 40 percent, a figure representing those grains that are collapsed and shriveled and that remain unstained in iodine-potassium iodide solution. Pollen sterility in both putative parents is less than 1 percent.

DISCUSSION

Current evidence from the collections and observations made in Queensland populations strongly suggests that hybrid *Lumnitzera littorea* × *racemosa* occurs as occasional individuals when the parental species grow together. The suggestion that this taxon may have been recognized earlier by Gaudichaud-Beaupré and called *L. rosea* is a reasonable hypothesis, but it rests entirely on the circumstantial evidence of petal color as he recorded it, since floral morphology is not illustrated in the necessary detail. The zygomorphic vs. actinomorphic condition, which would permit a clearer assessment of the specimen to which Gaudichaud-Beaupré referred, is not indicated in his illustrations. Indeed, the existence of zygomorphy in *L. littorea*, recognized and clearly illustrated by Brandis (1883), has been obscured in subsequent accounts. Zygomorphy is not a peculiarity of Queensland populations since it has also been seen by one of us (P. B. T.) in both Fiji and New Guinea. It is one part of the syndrome of characters that relates to the probable bird-pollination mechanism of this species, and

that contrasts it with the insect-pollination of *L. racemosa*. This difference in pollination mechanism may be sufficient to provide a specific sterility barrier that normally operates despite the fact that the species are often associated. Occasionally this barrier is broken, and hybrids may appear, although they are likely to be regarded as a pink-flowered form of either *Lumnitzera littorea* or *L. racemosa*, depending on the position of the inflorescence.

A problem in our use of this name is that Gaudichaud-Beaupré described and illustrated a plant with axillary inflorescences.[3] This could be explained if it is accepted that inflorescence position is not always dominant in the cross. A test of our hypothesis would be an artificial cross, which will be attempted.

Breakdown of the mechanism of isolation could be the result of bees and wasps visiting the two species successively, as our field observations show is possible. Persistence of hybrids in *Lumnitzera* is facilitated by vegetative spread that results from rooting of pendulous lower branches. A fairly extensive survey of mangrove populations in northern Queensland has not revealed any further populations of *L.* × *rosea* (although the two parent species are common), but does show minor variants in floral morphology. Populations of *L. littorea* at Jacky Jacky Creek have flowers with somewhat spreading petals. This might be the result of introgression from *L. racemosa*.

Future research is designed to substantiate our very incomplete observations on the floral biology and ecology of the putative parents and to provide cytological documentation that will advance our statements beyond the hypothetical.

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TRANSFER OF THE BRAZILIAN TRIXIS ERYNGIOIDES TO PEREZIA (COMPOSITAE, MUTISIEAE)

JORGE VICTOR CRISCI AND CLODOMIRO MARTICORENA

IN THE COURSE of a revisionary study of the South American species of the genus *Trixis* Browne (Compositae tribe Mutisieae subtribe Nassauviinae), *Trixis eryngioides* Cabrera, a species occurring in southeastern Brazil, seemed to be out of place. A careful study of this species and of all the genera of this subtribe convinces us that *Trixis eryngioides* must be transferred to the genus *Perezia* Lagasca.

A description of the plant, illustrations, pollen analysis, and discussion of the relationships of this taxon are presented here.

The abbreviations for herbaria listed in the citations of specimens are taken from the fifth edition of the *Index Herbariorum* (Lanjouw & Stafleu, 1964).

MATERIAL AND METHODS

Some of the pollen grains were acetolyzed according to the method outlined by Erdtman (1960); others were placed in 95 percent ethanol, stained with basic fuchsin, and mounted in glycerine jelly. For scanning electron microscopy (SEM) the acetolyzed pollen grains were used. After acetolysis the pollen samples were washed several times in glass-distilled water to remove traces of acids. Each sample was dispersed in a drop of ethanol (95 percent) and placed on a specimen holder. The samples were then air dried, coated with 50 Å to 100 Å carbon and about 200 Å to 300 Å gold-palladium alloy for conductivity. Finally, the specimens were photographed using a high-resolution SEM (JEOL JK II) at the Servicio de Microscopía Electrónica de Barrido del Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina.

The preparation of the material for sections was made according to the Leins technique (Leins, 1968) with the modifications made by Parra and Marticorena (1972). The sections of ca. 0.5 μm. were made with an AO Spencer microtome adapted for ultrathin sections and using glass blades.

Perezia eryngioides (Cabrera) Crisci & Marticorena, comb. nov. FIGURES 1–6.

Trixis eryngioides Cabrera, Bol. Soc. Argent. Bot. 7: 196. *fig. 5*. 1959.

Robust rosette plants, 60–70 cm. long, erect, from a taproot. Flowering stems terete, 5–7 mm. in diameter, slightly striated, glabrate, bearing 10 to 30 cauline leaves. Cauline leaves alternate, sessile, amplexicaul, ovate-lanceolate, acute, dentate, glabrate, 6–12 cm. long, 2–2.5 cm. wide. Basal leaves usually numerous, lanceolate, acute, amplexicaul, spinulose-dentate,

FIGURE 1. *Perezia eryngioides* (from *Smith & Klein 7777*): A, habit of plant, × ¼; B, capitula, × 1; C, corolla, × 2.5; D, achene and pappus, × 2.5.

glabrate, 20–34 cm. long, 3–4 cm. wide. Inflorescence a branched terminal cyme; pedicels 1–2 cm. long, surface with glandular trichomes. Individual capitula campanulate, 10–12 mm. long, 12–15 mm. wide. Involucre hemispheric, formed by 2 rows of bracts; involucral bracts lanceolate, acute at apex, 8–12 mm. long, 1.5–2 mm. wide, abaxial surface pubescent, adaxial surface glabrous, inner bracts scarious at the base and along the margins. Receptacle slightly concave, pubescent. Flowers about 20; corolla white. bilabiate, 8–15 mm. long; tube broader toward the apex, 5–7 mm. long, 0.3 mm. in diameter at the base and 1 mm. at the apex; outer lip lanceolate, liguliform, with 4 veins, apex 3-toothed, 4–8 mm. long, 1.5–2 mm. wide; inner lip bifid, acute at apex, 2.5–3 mm. long; stamens 5, glabrous, the filaments inserted at a point halfway from the base of the tube; anthers connate, 4–4.5 mm. long, with oblong apical appendage, tailed at base. Style bifid, its branches 1–1.3 mm. long, truncate, with a crown of elongate collecting hairs at the apex, papillose with shorter hairs on the adaxial surface, glabrous on the abaxial surface. Achenes turbinate, 2.5–3

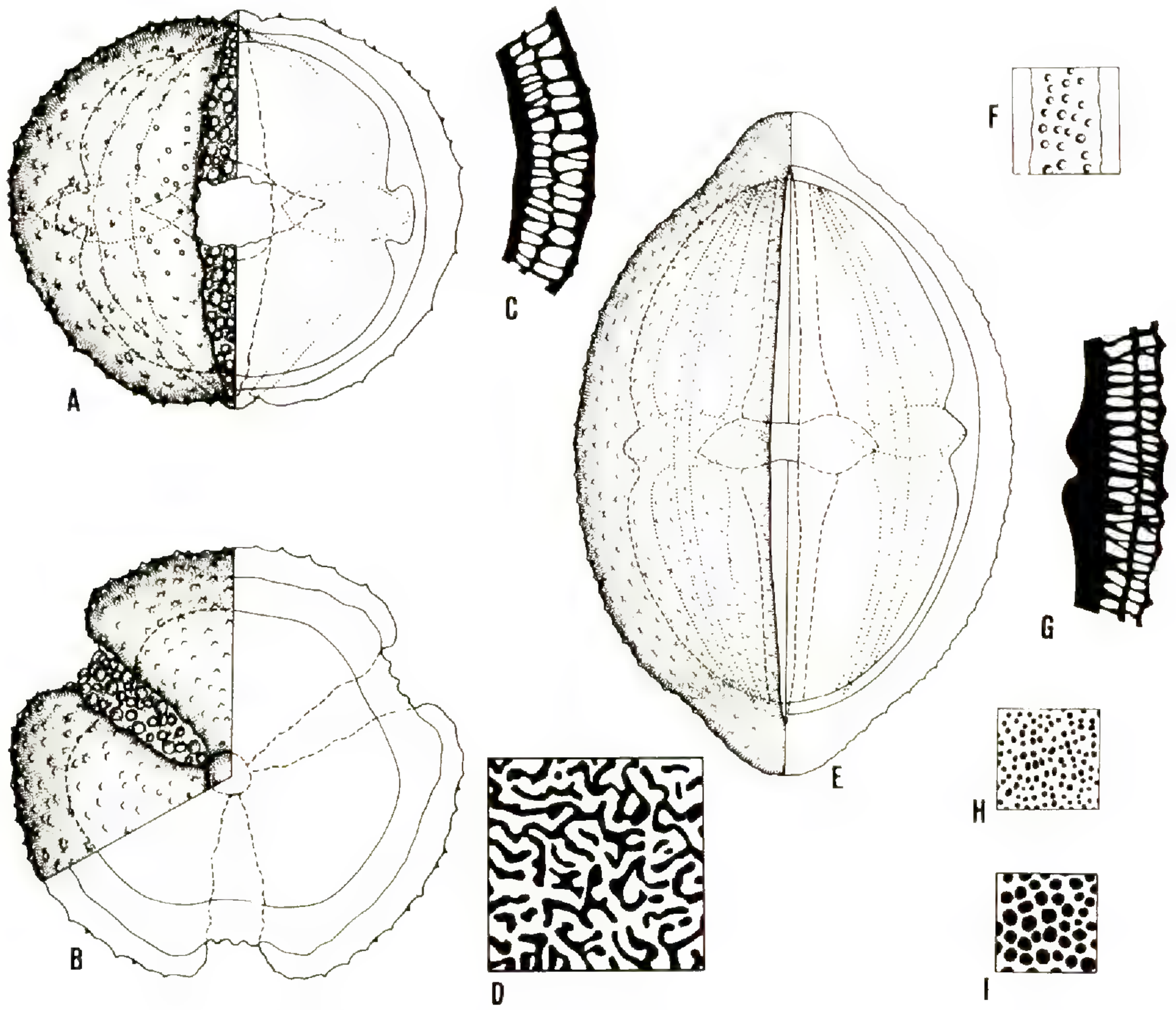
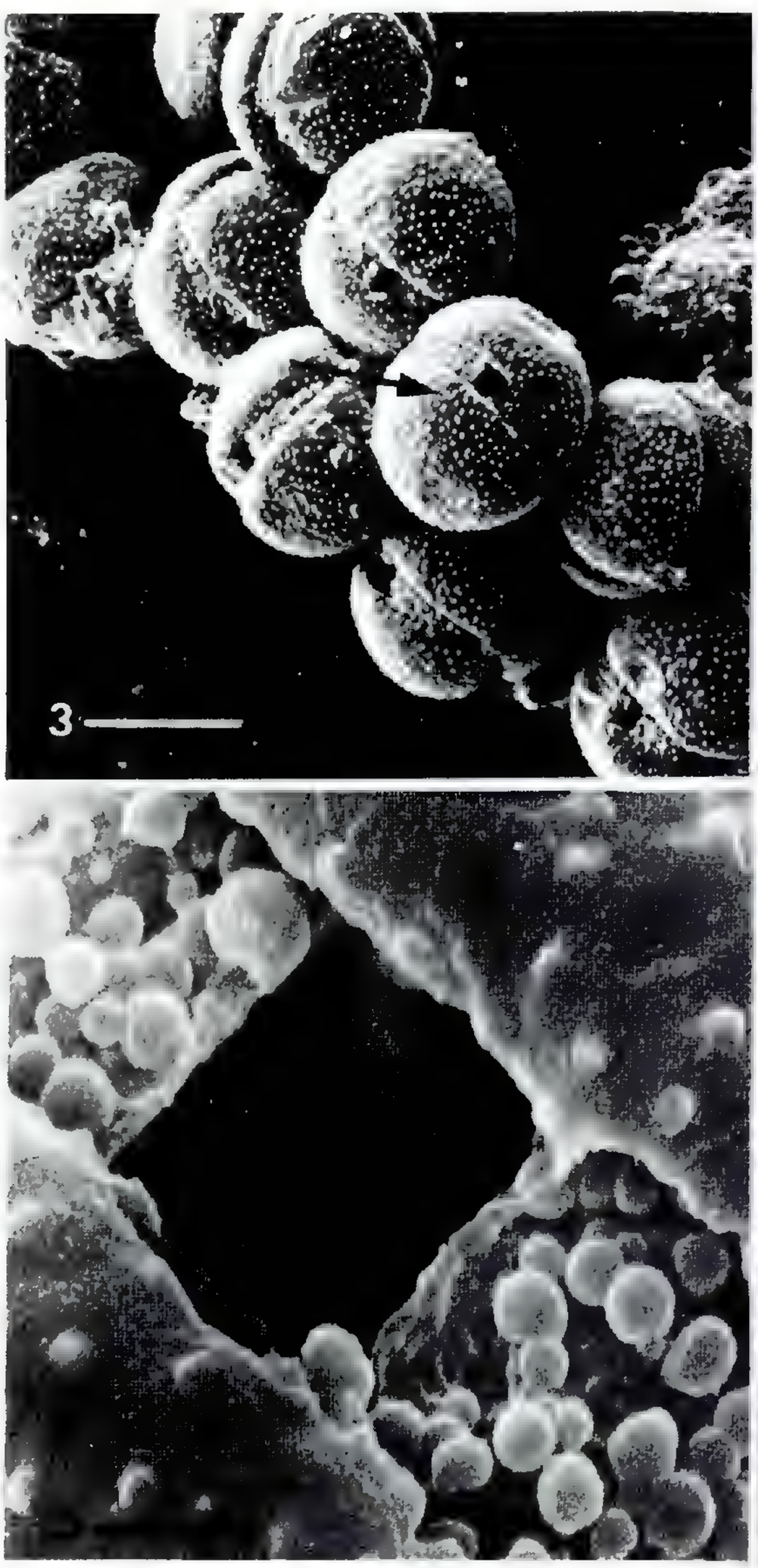
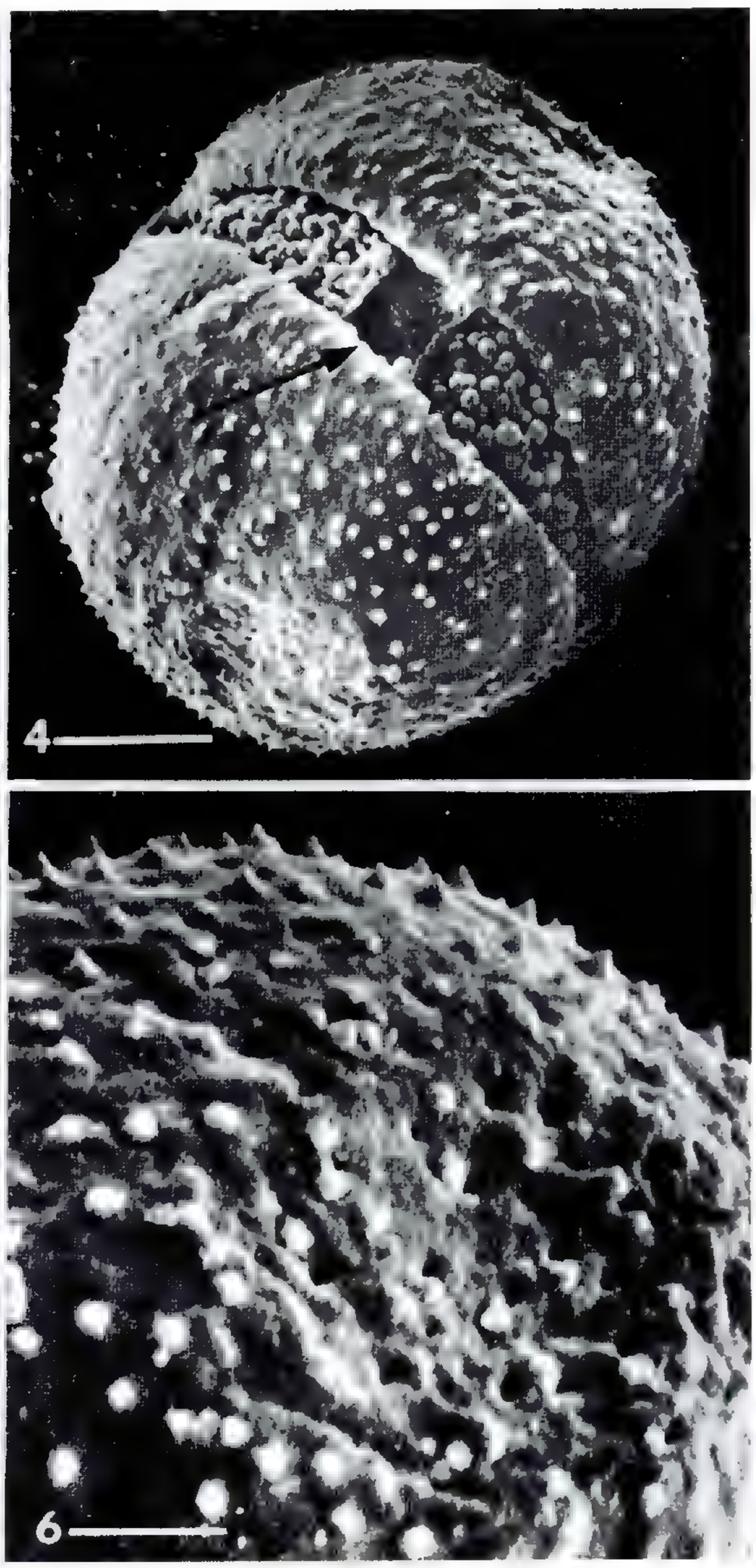


FIGURE 2. Pollen. A–D, *Perezia eryngioides* (from *Smith & Klein 7777*): A, equatorial view, × 1250; B, polar view, × 1250; C, cross section showing exine stratification, × 2000; D, pattern formed by bacula of tectum, × 2000. E–I, *Trixis alata* (from *Fröderstrom & Hultén 202*): E, equatorial view, × 1250; F, membrane of colpi with spherical processes, × 2000; G, cross section showing exine stratification, × 2000; H, pattern formed by bacula of tectum, × 2000; I, pattern formed by bacula of infratectum, × 2000.





FIGURES 3–6. Scanning electron micrographs of pollen of *Perezia eryngioides* (from *Smith & Klein 7777*): 3, several acetolyzed grains, arrow indicates the one shown in Figure 4, scale bar = ca. 20 μm.; 4, equatorial view, arrow pointing toward germ pore shown in Figure 5, scale bar = ca. 6.5 μm.; 5, germ pore and portion of surface of membrane of colpi (showing spherical processes), scale bar = ca. 2 μm.; 6, surface, showing conical spinules, scale bar = ca. 2.5 μm.

mm. long, 1–1.5 mm. wide, covered with double hairs. Pappus of numerous dark brown setose hairs, 7–10 mm. long, in 2 series.

Pubescence of two kinds of trichomes: (1) *glandular biseriate* (25–50 μm.) — multicelled (borne on leaves, stem, receptacle, involucre, and sparsely on the achenes); and (2) *double hairs* or "Zwillingshaare" (Hess, 1938) (120–150 μm.) — two cells joined along their inner walls but not meeting at the apices, copper colored (on the achenes).

POLLEN. Grains 3-colporate, exceptionally parasyncolpate, spheroidal-oblate to spheroidal-prolate, 28–34 × 29–35 μm. Apocolpium 2.5–3.5 μm. in diameter, slightly prominent to plane, rarely slightly depressed. Colpi

3–4.5 μm. wide, with margins entire or slightly curled, extremes obtuse to acute; membrane of the colpi with notable spherical processes, 0.5–1.2 μm. in diameter. Lalongate ora 2.3–5 μm. in external polar diameter, 4.7–5 μm. in internal polar diameter, and 10–16 μm. in equatorial diameter; equatorial extremes acute. Amb rounded. Exine crassisexinous, pertectate, spinulose, 2.5–3 μm. thick at the pole, 3–5 μm. at the equator. Spinules conical, ca. 0.5 μm. high. Terminal membrane ca. 0.5 μm. thick. Bacula usually laterally fused, forming curled internal walls and leaving spaces of labyrinthic shape. Tectum and infractectum separated from each other by a thin layer not parallel to the nexine (zigzag). Infratectum 1–1.3 μm. thick, baculate in a similar fashion to the tectum. Nexine ca. 0.7 μm. thick.

DISTRIBUTION. Southeastern Brazil, province of Santa Catarina, in Bom Retiro, Irani, and Lajes municípios, from 700 to 1700 meters altitude. Flowering from October to December.

SPECIMENS EXAMINED. **Brazil.** SANTA CATARINA: Bom Retiro, Fazenda Campo dos Padres, dwarf forest, 1650 m., *L. B. Smith & R. M. Klein 7777* (LP, holotype of *Trixis eryngioides* Cabrera); Lajes, Painel banhado, 950 m., *Klein 4566* (LP); Irani, Campo de Irani, bog, 700–900 m., *Smith & Klein 13031* (LP).

Perezia eryngioides has been collected very few times and seems to be rare. It is found in humid places in the western zone of the "campo" or prairie flora (Smith, 1962) of southern Brazil.

RELATIONSHIPS OF PEREZIA ERYNGIOIDES

Perezia eryngioides is a member of tribe Mutisieae subtribe Nassauviinae, which has characteristic bilabiate corollas with the outer lip three-toothed and the inner lip bifid; anthers long tailed at the base; and style bifid with branches truncate at the apex (Crisci, 1974).

Perezia eryngioides was described as a species of *Trixis*; it is, however, very different from the other species of this genus, as is indicated in TABLE 1.

In addition to the criteria shown in TABLE 1, there are a number of other features that may be labeled "tendencies" common to some species of *Trixis* but from which there are exceptions: pubescence including woolly trichomes, capitula with less than 15 flowers each, leaves very short-petiolate or subsessile.

Trixis P. Browne [1] is a genus of about 50 species of shrubs occurring from Mexico to central Argentina and in the West Indies. There are two centers of diversity, one in southwestern Mexico, the other in southern Brazil, northern Argentina, and Uruguay (Anderson, 1972; Cabrera, 1936; Loja, 1969).

Perezia eryngioides is better placed in *Perezia* since it shares with the species of this genus an herbaceous habit, basal rosettes, achenial trichomes, white corollas (in *Perezia* the color of corollas is variable but

[1] Hist. Jamaica, 312. 1756. TYPE SPECIES: *Trixis inula* Crantz.

TABLE 1. **A comparison of the genus Trixis and Perezia eryngioides.**

	Trixis	*Perezia eryngioides*
HABIT	Shrubs; not rosette plants	Perennial herbs; rosette plants
COROLLA	Bright yellow	White
DOUBLE HAIRS ON ACHENES	Colorless, ca. 150–200 μm. long, oblong in shape, obtuse at apex, less than 5 times longer than wide, releasing mucilage when wet	Copper colored, ca. 120–150 μm. long, linear in shape, short-bifid at apex, at least 20 times longer than wide, not releasing mucilage when wet
POLLEN	Prolate (rarely subprolate); exine with infratectum thicker than tectum and separated from it by a thick layer parallel to nexine (see FIGURE 2)	Oblate-spheroidal to prolate-spheroidal; exine with tectum thicker than infratectum and separated from it by a thin layer not parallel to the nexine (zigzag)

never bright yellow), and pollen morphology, including exine stratification. Also, both have more than 15 flowers per capitulum.

Perezia Lagasca [2] is a genus of 32 species of herbs, 27 occurring in the Andean region of South America and 5 (including *P. eryngioides*) in lowland open woods of Paraguay, Uruguay, Brazil, and Argentina (Vuilleumier, 1969; Cabrera & Klein, 1973; Crisci, 1974).

Vuilleumier (1969; 1973 as B. Simpson) clustered the species of *Perezia* into six well-defined groups: Prenanthoides, Coerulescens, Magellanica, Recurvata, Pungens, and Multiflora.

One of the most distinctive and well-defined groups centers around *Perezia multiflora* and consists of four species: *P. multiflora* (H. & B.) Less. (with 2 subspecies, *multiflora* and *sonchifolia*); *P. squarrosa* (Vahl) Less. (with 2 subspecies, *squarrosa* and *cubataensis*); *P. kingii* Baker, and a species described since Vuilleumier's paper, *P. catharinensis* Cabrera. All of the species of this assemblage are found exclusively or have populations in the Paraguay-southern Brazil-Uruguay basin, although *P. multiflora* itself has its main center of distribution in the high, dry puna of Peru and Bolivia.

Within the genus, the four species of this group share the unusual characters of silky, copper-colored achenial trichomes, reduced number of involucral bracts, pubescence on the receptacle, and small pollen size (24–30 μm.). In addition, there are a number of features that are not exclusive to the Multiflora group such as small head size, compacted head clusters, taproots rather than rhizomatous rootstocks, and spiniferous foliage.

Members of the Multiflora group possess the lowest chromosome numbers in the genus, including the probable base number $x = 4$ (Vuilleu-

[2] Am. Nat. 1: 311. 1811. TYPE SPECIES: *Perezia magellanica* (L. f.) Lagasca (= *Perdicium magellanicum* L. f.).

mier, 1969), suggesting that this group is a primitive one in the genus. However, as was pointed out by Vuilleumier (*op. cit.*), it does not appear to represent the basal complex, but seems rather to be a closely knit cluster of species that radiates in southeastern Brazil from a very early offshoot of the main ancestral stock.

Perezia eryngioides belongs to the Multiflora group since it possesses all the characters that define the assemblage.

Although the Multiflora group is a very tightly knit assemblage, *Perezia eryngioides* seems to be more closely related to *P. squarrosa* (especially subsp. *cubataensis*) than either of these two species is to *P. kingii*, *P. catharinensis*, or *P. multiflora*. The two taxa are sympatric in the *P. eryngioides* range and can be distinguished on the bases of corolla color and basal leaf size. *Perezia squarrosa* is found in humid places in southern Brazil, Paraguay, and Uruguay, at low elevations and even at sea level.

To summarize, we can establish that *Perezia eryngioides* is easily distinguished from all the species of *Trixis* by its herbaceous habit, white corollas, characteristic achenial trichomes, and pollen morphology, including exine stratification. It shares these characters with the species of the genus *Perezia*. From most of the species of *Perezia*, it can be distinguished by the color of its achenial trichomes, the reduced number of involucral bracts, the pubescence of the receptacle, and the small size of its pollen grains, characters it shares with *P. multiflora*, *P. kingii*, *P. catharinensis*, and *P. squarrosa*. It can be distinguished from these four species as shown in the following key.

A. Capitula less than 10 mm. long.
  B. Involucral bracts with small white spines near the base; pappus pure white. ..... *P. kingii.*
  B. Involucral bracts without spines; pappus brown. ..... *P. catharinensis.*
A. Capitula longer than 10 mm.
  C. Capitula hemispheric; florets bicolored, with yellow on the inner part of the corolla tube and the inner petals; heads often congested. ..... *P. multiflora.*
  C. Capitula campanulate; florets monochromatic; heads in a loose cyme.
    D. Basal leaves 4–20 cm. long, 0.5–2.5 cm. wide; corollas blue, violet, or reddish. ..... *P. squarrosa.*
    D. Basal leaves 20–34 cm. long, 3–4 cm. wide; corollas white. ..... *P. eryngioides.*

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A REVISION OF THE WEST INDIAN VERNONIAS (COMPOSITAE)

STERLING C. KEELEY

VERNONIA IS A widely distributed genus with nearly 1000 species, half of which are found in tropical areas of the New World. The diversity inherent in such a wide-ranging group has caused numerous problems in its systematics and taxonomy. The West Indian vernonias have been particularly troublesome in this regard due to their variable vegetative features and the apparent close relationships among species. Gleason provided the first comprehensive treatment of taxa in the West Indies in his 1906 revision of the North American Vernonieae. Ekman (1914) also studied and revised the West Indian vernonias, but disagreed with many of Gleason's specific and subsectional assignments. Since Gleason updated his earlier revision in 1922, several new species have been described in isolated publications, but no effort has been made to evaluate the merit of overall taxonomic relationships or treatments.

Prior to the treatments of Gleason and Ekman, major contributions to *Vernonia* taxonomy in the West Indies were made by Grisebach (1861, 1862, 1866, 1879), Lessing (1829, 1831), de la Sagra (1850), Schultz-Bipontinus (1847, 1863), and Urban (1899, 1903, 1911, 1912). A complete history of the tribe Vernonieae and its subsections is given in Jones (1977).

The present study has encompassed a period of several years during which observations and collections were made in the field, greenhouse accessions were grown and studied, and loans from major herbaria were examined. The main descriptive and revisionary aspects presented here are drawn from more than 2500 specimens from eight herbaria, but species concepts were strongly molded by field observations. Forty-two species are treated here; keys and synonymies are provided. Evolutionary and biogeographic comparisons are not treated because relationships with mainland taxa are presently unknown.

MATERIALS AND METHODS

Loans of herbarium material were obtained from F, GH, MO, NY, S, TEX, and US. Additional type material was generously provided by B, BM, GOET, K, L, M, and P. Population samples were collected during December, 1974 (Jamaica, Hispaniola, Puerto Rico), and December, 1975 (Jamaica, the Lesser Antilles, Trinidad). Greenhouse accessions were established from achenes and/or rootstocks collected during these trips and were used to obtain material for chromosome counts and morphological comparisons.

Twenty-five to one hundred herbarium specimens were selected and scored for each putative taxon examined, except where fewer than twenty-five specimens were available, in which case all specimens were scored. In

scoring those taxa with large available collections, the number studied depended on the degree of taxonomic confusion and on the variability of the material. Local populations collected in the field were also scored to obtain a measure of variation due to environmental factors. The number of individuals available for this type of comparison varied widely and was determined by distribution and accessibility.

Herbarium and field-collected specimens were measured or scored for the following characters: plant height, leaf blade length and width and ratio of these two measurements, petiole length, involucre height and width, inner phyllary length and width, number of flowers per head, achene length and surface, inner and outer pappus length, corolla length, and anther length. Midcauline leaves were selected for measurement on each specimen. Only fully matured heads were used for measurements of length and width of involucres and phyllaries. Anther length and corolla length were measured on soaked, fully mature flowers. Means and ranges were determined for the numerical values of each character. An attempt was made to use the descriptive terms of Featherly (1954) and the shapes outlined by Lindley (1848, pp. 345–383).

RESULTS AND DISCUSSION

Characters scored and ranges of numerical values are given in the species descriptions. Distributions were determined from herbarium specimens and field collections. Representative specimens are cited for each species, but the lists have been kept brief. Distributions are shown on maps. A complete list of exsiccatae is available from the author on request; all specimens examined have been annotated.

Chromosome counts were determined using the standard aceto-carmine squash technique with pollen mother cells (PMC's). Most taxa are diploid $n = 17$, but one hexaploid species, *Vernonia trinitatis*, was discovered. Chromosome numbers, when available, follow the species descriptions.

Species treatments and subsectional assignments differ in many cases from those of Gleason (1906, 1922) and Ekman (1914). The number of species recognized has been reduced from 60 (Gleason, 1922) and 61 (Ekman, 1914) to 42 in this treatment. Subsectional differences have been detailed, and a comparison is presented elsewhere (Keeley & Jones, 1977a). The range of major West Indian subsections and the general morphology of the inflorescence of taxa in each subsection are shown in FIGURE 1.

Keys to sections and subsections are presented first as an aid to identification. This key is followed by keys to the species within each subsection.

KEY TO SECTIONS AND SUBSECTIONS OF WEST INDIAN VERNONIA

A. Plants annual; sect. TEPHRODES: one widely distributed, pantropical weed. ..... 42. *V. cinerea.*

A. Plants perennial; sect. LEPIDAPLOA.

B. Herbaceous perennial. VII. subsect. PANICULATAE: one species, Florida and the Bahamas. ..... 41. *V. blodgettii.*

B. Suffruticose perennials, restricted to the West Indies.
C. Achenes glabrous or resinous, ca. 4 mm. long.
D. Achenes 3- or 4-angled or with faint ribs; involucres campanulate. ..... IV. subsect. SAGRAEANAE.
D. Achenes 8- or 9-ribbed; involucres turbinate. ..... II. subsect. BUXIFOLIAE.
C. Achenes pubescent, 2–3 mm. long.
E. Leaves membranous, glabrous or minutely pubescent on both surfaces, margins serrate. V. subsect. PALLESCENTES: one species, St. Vincent. ..... 39. *V. pallescens.*
E. Leaves more or less coriaceous, pubescent especially on lower surface, margins entire to remotely denticulate.
F. Inflorescence a dense scorpioid cyme, sometimes appearing corymbose; heads rarely subbracteate.
G. Corollas smooth, occasionally resin dotted. ..... III. subsect. POLYANTHES.
G. Corollas with prominent hairs in clefts of corolla lobes. VI. subsect. SCORPIOIDES: one species, Trinidad and Haiti. ..... 40. *V. scorpioides.*
F. Inflorescence an open scorpioid cyme, or if condensed then not corymbose; heads usually subbracteate. ..... I. subsect. ARBORESCENTES.

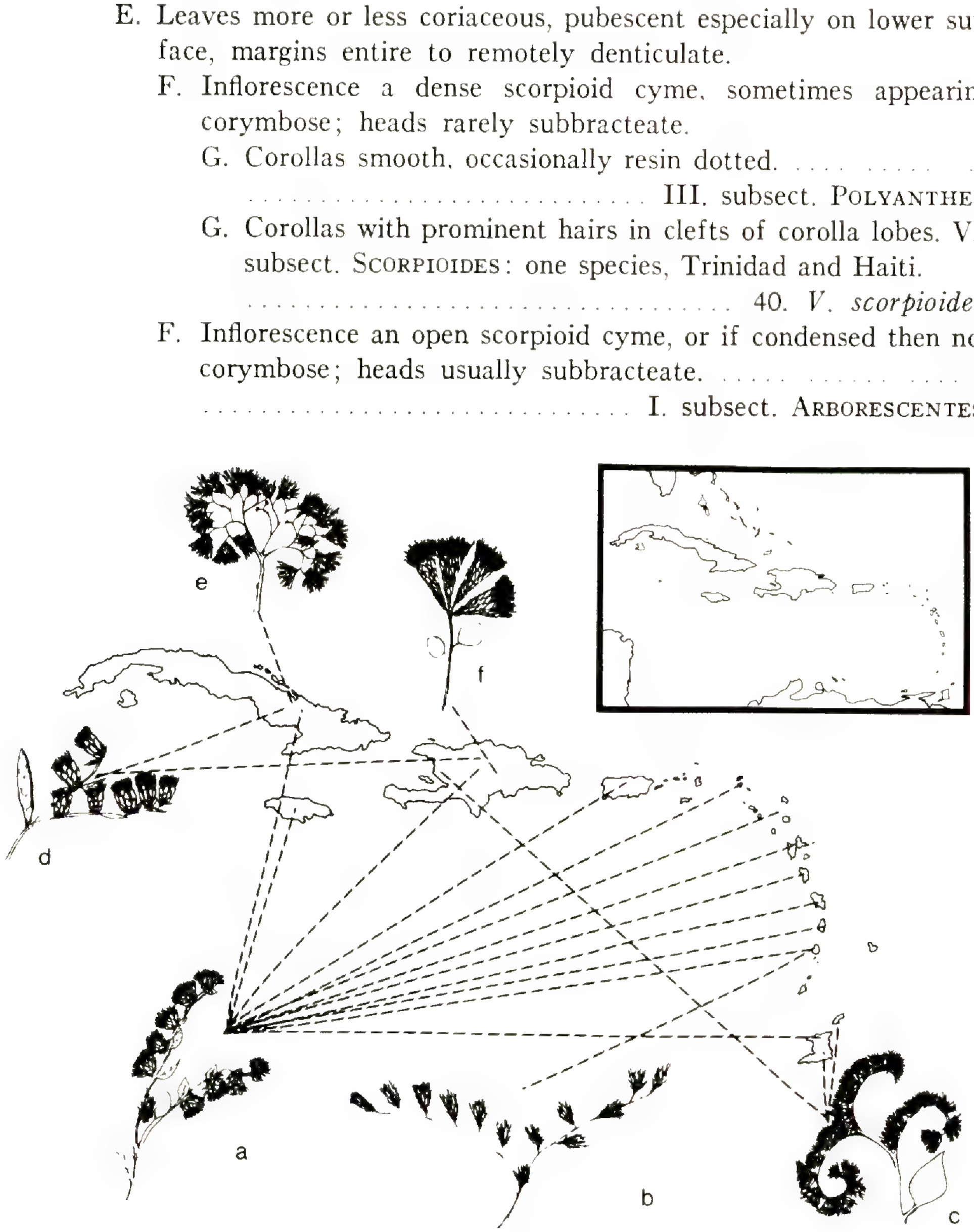


FIGURE 1. Distribution and general morphology of subsections of *Vernonia* section LEPIDAPLOA in the West Indies: ARBORESCENTES (a), PALLESCENTES (b), SCORPIOIDES (c), SAGRAEANAE (d), POLYANTHES (e), and BUXIFOLIAE (f).

KEY TO SUBSECTION I. ARBORESCENTES

A. Pappus white.
B. Leaves linear or narrowly linear-lanceolate.
C. Leaves shiny-pustulate above, glandular with pronounced pubescence on veins of lower surface. ..... 25. *V. commutata.*
C. Leaves pubescent, white-strigose above, sericeous with inconspicuous pubescence on veins of lower surface. ..... 24. *V. stenophylla.*
B. Leaves orbicular, ovate, lanceolate, obovate to oblanceolate.
D. Heads solitary; leaf margins conspicuously repand; maritime cliffs, Cuba. ..... 22. *V. complicata.*
D. Heads in cymes or clusters; leaf margins various but not conspicuously repand; various habitats throughout the West Indies.
E. Flowers per head 5 to 7. ..... 5. *V. segregata.*
E. Flowers per head 10 or more.
F. Leaves ovate, orbicular, obovate to obcordate, less than 3(5) cm. long.
G. Plants low-growing shrubs, sprawling; petioles less than 1 mm. long; Hispaniola. ..... 21. *V. fruticosa.*
G. Plants upright shrubs; petioles more than 1 cm. long; various locations in the West Indies.
H. Leaves crowded on terminal branches, gray-green, white-tomentose below; Bahamas. ..... 23. *V. arbuscula.*
H. Leaves evenly spaced along stems, yellow-green, glandular, closely pubescent below; Cuba.
I. Involucres 11–12 mm. high; phyllaries purple, narrowly and stiffly lanceolate. ..... 18. *V. pineticola.*
I. Involucres 3–6 mm. high; phyllaries gold to brown, deltoid to ovate or lanceolate, but not stiffly so. ..... 13. *V. orbicularis.*
F. Leaves ovate, ovate-lanceolate to lanceolate or oblanceolate, more than 5 cm. long.
J. Stems round, faintly ribbed, closely pubescent, and conspicuously green even when old; Trinidad. ..... 12. *V. trinitatis.*
J. Stems distinctly ribbed, variously pubescent, becoming glabrate with age, gray to brown; various locations throughout the West Indies.
K. Phyllaries loosely imbricate in few series; achenes partially exposed even in immature heads. ..... 20. *V. gnaphaliifolia.*
K. Phyllaries firmly imbricate in at least five series; achenes concealed except in fully matured, reflexed heads.
L. Involucres 6–11 mm. high.
M. Phyllaries in more than six series; involucres long-campanulate or turbinate. ..... 17. *V. desiliens.*
M. Phyllaries in five or fewer series; involucres broadly campanulate.
N. Corollas 5.5–9 mm. long; anthers less than 2 mm. long.

O. Phyllaries pale yellow-green, tips recurved. ..... 15. *V. jenssenii.*
O. Phyllaries gold to brown, tips erect or if curved not uniformly so. ..... 14. *V. leptoclada.*
N. Corollas 9 mm. or longer; anthers more than 2 mm. long. ..... 19. *V. yunquensis.*
L. Involucres less than 5(6) mm. high.
P. Leaves glabrate, resinous above, with prominently pubescent veins on lower surface. ..... 16. *V. urbaniana.*
P. Leaves pubescent, resinous, with trichomes on lamina and veins of lower surface.
Q. Anthers 2.5–3 mm. long; phyllaries uniformly tawny, often with a strong central nerve extending into the tip; Martinique, St. Lucia, St. Vincent. ..... 11. *V. arborescens.*
Q. Anthers ca. 2 mm. long; phyllaries gold to brown, with dark tips, lacking a strong central nerve; various locations throughout the West Indies.
R. Leaves oblong to lanceolate, sparsely pubescent above and below; Guadeloupe. ..... 7. *V. albicaulis.*
R. Leaves ovate to elliptic, densely pubescent at least on younger leaves; Jamaica, Cuba. ..... 10. *V. divaricata.*
A. Pappus brown or tawny.
S. Leaves whorled; plants sprawling. ..... 3. *V. verticillata.*
S. Leaves alternate; plants upright.
T. Leaves broadly ovate to orbicular, the apex blunt, rarely acute.
U. Phyllaries imbricate in ten or more spiral series; leaf margins densely white-pubescent. ..... 4. *V. rigida.*
U. Phyllaries imbricate in five or fewer series, not conspicuously spiraled; leaf margins glabrous, not white. ..... 2. *V. harrisii.*
T. Leaves elliptic to oblong or long-ovate, the apex acute to acuminate, occasionally obcordate.
V. Flowers per head less than 8; Blue Mts., Jamaica. ..... 6. *V. pluvialis.*
V. Flowers per head more than 10; various locations.
W. Leaves glabrous or sparsely pubescent, not rugose, the apex acuminate, rarely acute; Jamaica. ..... 1. *V. acuminata.*
W. Leaves pubescent, at least on lower surface, often rugose, apex acute to obcordate; not in Jamaica.
X. Flowers per head ca. 18; plants sprawling to vinelike; inflorescence of zigzag cymes. ..... 9. *V. borinquensis.*
X. Flowers per head ca. 12(15); plant suffrutescent; inflorescence of smooth cymes.
Y. Anthers less than 1.5 mm. long; leaves dark green and sparsely pubescent above, white-sericeous below, linear to lanceolate. ..... 8. *V. sericea.*
Y. Anthers more than 2 mm. long; leaves green on both surfaces, minutely pubescent to glabrous above and below, ovate to lanceolate, occasionally obcordate. ..... 7. *V. albicaulis.*

KEY TO SUBSECTION II. BUXIFOLIAE

A. Pappus of two equal series of bristles, appearing as one. . . . . 26. *V. barkeri.*
A. Pappus of two series of bristles, the outer series ca. 1/10 as long as the inner.
  B. Corollas more than 9–11 mm. long; leaves sessile or with resin-dotted petioles to 0.5 mm. long; pappus yellow-orange. . . . . 27. *V. buxifolia.*
  B. Corollas 6–8 mm. long; petioles 1–2 mm. long, not conspicuously resinous; pappus yellow to pink. . . . . 28. *V. tuerckheimii.*

KEY TO SUBSECTION III. POLYANTHES

A. Corollas resinous; petioles 8–15 mm. long. . . . . 31. *V. menthaefolia.*
A. Corollas glabrous; petioles 1–6(–8) mm. long.
  B. Flowers per head 15 or more; pappus white or very pale tawny. . . . . 29. *V. havanensis.*
  B. Flowers per head less than 10; pappus yellow-brown. . . . . 30. *V. hieracioides.*

KEY TO SUBSECTION IV. SAGRAEANAE

A. Flowers per head 38 to 66. . . . . 32. *V. aronifolia.*
A. Flowers per head 30 or less.
  B. Involucres narrowly cylindrical; flowers per head 4 to 8. . . . . 33. *V. purpurata.*
  B. Involucres campanulate; flowers per head 9 to 16.
    C. Leaves rugose, shining, glabrate and scabrous above, hirsute to tomentose below.
      D. Leaves with prominent, pubescent veins on lower surface, sparsely pubescent to glabrate on lower surface of lamina, oblanceolate to lanceolate, widest above the middle, length to width ratio ca. 3. . . . . 34. *V. ekmanii.*
      D. Leaves without prominent veins, densely pubescent on lower surface, lanceolate, widest at or below the middle, length to width ratio ca. 5. . . . . 35. *V. sprengeliana.*
    C. Leaves coriaceous, not rugose, dull to shiny, generally pubescent above and below.
      E. Leaves with conspicuous long, white hairs above and below; corolla 10 mm. or longer. . . . . 36. *V. viminalis.*
      E. Leaves glabrous to minutely pubescent above, closely resinous-pubescent below; corolla 6–9 mm. long.
        F. Phyllary tips recurved, slightly pubescent; pappus white. . . . . 37. *V. wrightii.*
        F. Phyllary tips straight, villous; pappus brown to pink. . . . . 38. *V. sagraeana.*

VERNONIA Section LEPIDAPLOA
Subsection I. ARBORESCENTES

1. **Vernonia acuminata** Lessing, Linnaea **6**: 663, 664. 1831. TYPE: Ind. Occ. [Jamaica], *Swartz s.n.* (holotype, s!).

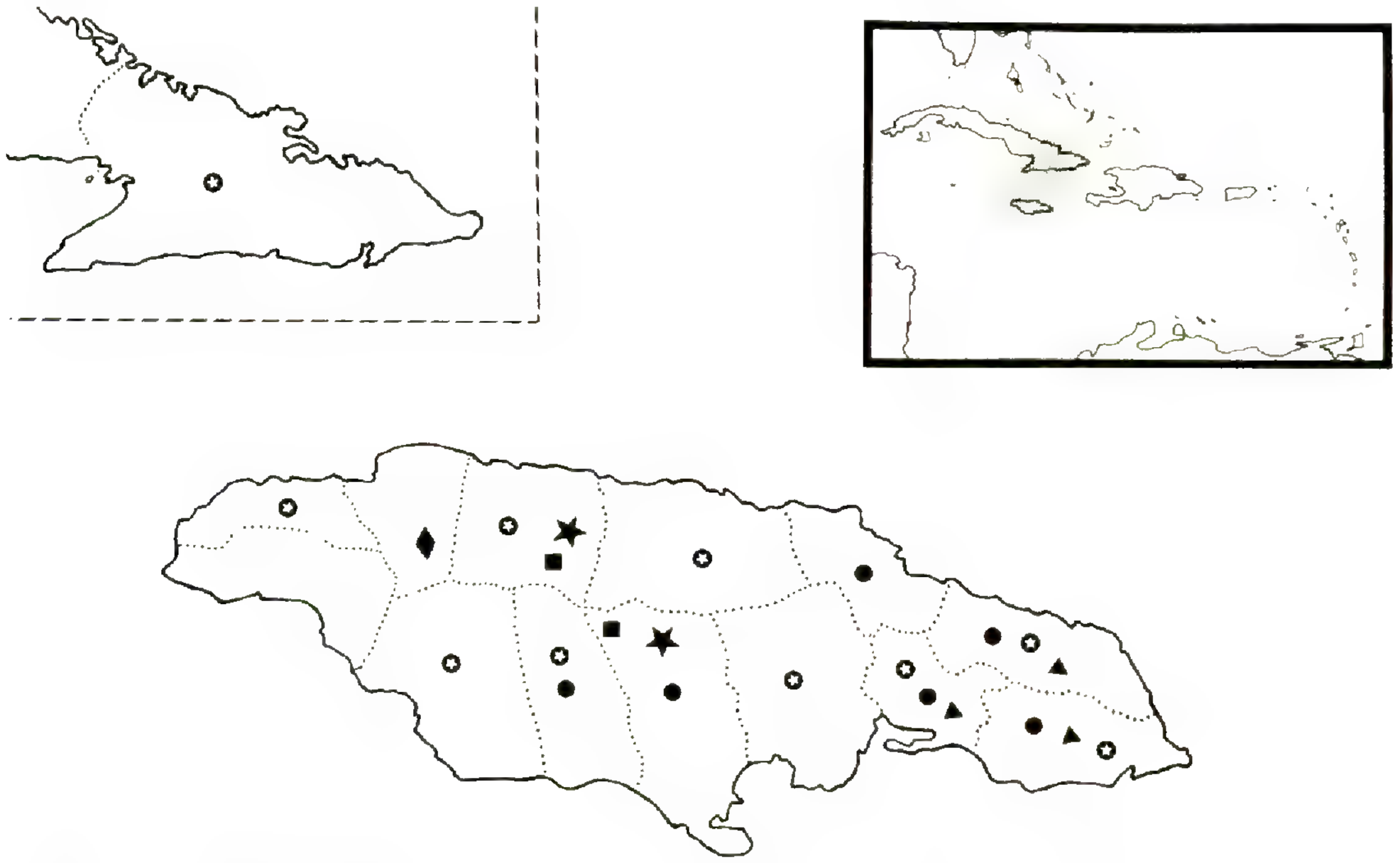
Vernonia divaricata de Candolle, Prodr. **5**: 48, 49. 1836, p.p., non *V. divaricata*

Swartz, 1806. TYPE: Ind. Occ. [Jamaica], *Swartz s.n.* (holotype, G-DC (IDC B–800–2. 773: II. 5!)).

Cacalia acuminata (Lessing) Kuntze, Rev. Gen. Pl. **2**: 969. 1891.

Vernonia expansa Gleason, Bull. N. Y. Bot. Gard. **4**: 186. 1906. TYPE: Jamaica. Trelawny Parish, near Troy, 6 Dec. 1940, *Harris 8796* (holotype, NY!; isotypes, F!, US!).

Shrub, 1–2 meters tall; stems pilose-hispid to sparsely hispid, ribbed. Leaves evenly spaced, at least along the main stem; petioles 2–5 mm. long, strigose to pilose-hispid; blades 4–7.5 cm. long, 1.5–2.8 cm. wide, length/width ratio ca. 2, widest at or slightly above the middle, elliptic to occasionally oval, gland dotted and sparsely pubescent to glabrate above, minutely pubescent and conspicuously gland dotted below, apically acuminate to acute, basally cuneate to rounded, margins entire. Inflorescences of condensed cymes, divaricate and often with elongated pedicels, indeterminate; heads often 9 to 12 per cyme, 10- to 18-flowered, sessile or with strigose to tomentose peduncles to 1 mm. long; involucres campanulate, 4–5 mm. high, 4–7 mm. wide, the phyllaries pubescent, not tightly appressed, golden brown to brown, the inner phyllaries lanceolate to rhomboid, 3–5.4 mm. long, 0.7–1.3 mm. wide, tips acute, the outer phyllaries ovate, 0.9–1.6 mm. long, 0.3–0.7 mm. wide; pappus brown, the inner bristles 3–5 mm. long, the outer pappus of fimbriate scales, 0.6–1.3 mm. long; corollas 4.5–6.5(–7.5) mm. long, white to pink, gland dotted in some, sometimes with a strong odor; anthers 1.5–2 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed. Chromosome number $n = 17$. Flowering and fruiting throughout the year, but mainly between January and March.



MAP 1. Distribution of *Vernonia acuminata* (solid circles), *V. divaricata* (circles with stars in centers), *V. harrisii* (squares), *V. pluvialis* (triangles), *V. rigida* (stars), and *V. verticillata* (diamond) in Jamaica, and Oriente Province, Cuba.

DISTRIBUTION. Open, wooded limestone hills, along roadsides, and on bauxite-containing soils, between 150 and 1650 meters, in Jamaica (MAP 1).

REPRESENTATIVE SPECIMENS. **Jamaica.** CLARENDON PARISH: Peckham Woods, *Proctor 8253* (NY). MANCHESTER PARISH: Marshall's Pen, *Proctor 29396* (TEX). PORTLAND PARISH: Seamen's Valley, *Maxon & Killip 66* (F, GH, NY, US). ST. ANDREW PARISH: mile post 12–12½ on Rock Hall Rd., *Adams 7016* (MO). ST. ANN PARISH: Reynolds Mine near Lydford P.O., *Howard, Proctor, & Stern 14593* (GH). ST. THOMAS PARISH: slopes of Curva Curva Gap, *Britton 4055* (NY).

This species is one of the two most common vernonias in Jamaica; it can easily be distinguished from the other common species, *Vernonia divaricata*, by its dark brown pappus and its glabrate leaves. *Vernonia acuminata* is similar to *V. harrisii* and is probably very closely related to it.

2. **Vernonia harrisii** S. Moore, Jour. Bot. 66: 164. 1928. TYPE: Jamaica. Clarendon Parish, Peckham Woods, 27 Dec. 1917, *Harris 12776* (holotype, BM!; isotypes, F!, GH!, K!, MO!, NY!, S!).

Shrub, 2–3 meters high; stems ribbed, covered with dense down. Leaves evenly spaced along main stem, more crowded terminally; petioles 3–6 mm. long, downy; blades 3.2–5 cm. long, 1.4–2.7 cm. wide, length/width ratio ca. 2, widest at or below the middle, broadly ovate, shiny, gland dotted, with short, stiff, sparse hairs above, hairs more numerous and prominent on veins below, apex rounded to acute, base rounded to cuneate, margins entire. Inflorescences of scorpioid cymes, variably extended; heads 9- to 12-flowered, sessile or with pubescent peduncles to 2 mm. long; involucres campanulate, 5–7 mm. high, 4–5 mm. wide, the phyllaries resin dotted on tips and near bases, variably pubescent, loosely appressed, reflexed at maturity, gold-brown, the inner phyllaries awl shaped to lanceolate, much narrower at the tip than at the base, 4.1–6 mm. long, to 1.2 mm. wide, with tips tapering, acute to acuminate, the outer phyllaries ovate to deltoid, 1–1.4 mm. long, 0.5–0.8 mm. wide; pappus brown, the inner bristles 4–5.5 mm. long, the outer pappus of fimbriate scales, 0.6–1.5 mm. long; corollas 5.5–7 mm. long, occasionally resin dotted near tips, lavender to purple, with no detectable odor; anthers 1.9–2.3 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed, some with resinous dots. Flowering and fruiting from December to March.

DISTRIBUTION. Steeply eroded limestone pinnacles, amid dense vegetation, from 500 to 800 meters, in two locations in Jamaica (MAP 2).

REPRESENTATIVE SPECIMENS. **Jamaica.** CLARENDON PARISH: wooded limestone hill, Peckham Woods, type locality, *Proctor 9766* (GH, US). TRELAWNY PARISH: Mango Tree Hill, along road between Burnt Hill and Spring Garden, *Proctor 31177* (MO, TEX).

This species is similar in leaf shape to some specimens of *Vernonia rigida*, with which it has been confused in the past. *Vernonia harrisii* has

many fewer rows of phyllaries, possesses smaller heads, and lacks the conspicuous white leaf edges of *V. rigida*. *Vernonia harrisii* appears to be most closely related to *V. acuminata* and may be a recent derivative of this more widespread species.

3. **Vernonia verticillata** Proctor ex Adams, Phytologia 21: 409. 1971. TYPE: Jamaica. St. James Parish, on wooded limestone hilltop, White Rock Hill, ca. 1 mi. S. of Sweetwater, small, spreading shrub, flowers bright purple, 2 Dec. 1962, *Proctor 22987* (holotype, IJ!; isotype, UCWI!).

Shrub, erect or sprawling, 2.5–3 meters tall; stems ribbed, with occasional resin glands. Leaves whorled, at least the cauline, usually with three leaves per node; petioles 1–3 mm. long, with short hairs and frequently with resin dots; blades 3.8–7 cm. long, 2–3 cm. wide, length/width ratio ca. 1.8, widest at or below the middle, ovate to elliptical, shiny, gland dotted, with few short hairs above and below, apex acute to acuminate, base rounded, margins entire. Inflorescences greatly compacted clusters of 3 to 10 heads, sometimes along a cyme; heads (4- to) 5- to 9-flowered, sessile or with gland-dotted, hispid to hirsute peduncles to 2 mm. long; involucres narrowly campanulate, 5–7 mm. high, (3–)4–

MAP 2. Distribution of *Vernonia albicaulis* subsp. *albicaulis* (solid circles) and subsp. *longistylis* (circles with stars in centers), *V. arborescens* (squares), and *V. pallescens* (triangles). Lower left inset, Guadeloupe and Marie-Galante; lower right inset, St. Vincent.

7 mm. wide, the phyllaries resin dotted at tips and bases, loosely appressed, brown to gold, some with dark tips, the inner phyllaries lanceolate, 4.5–6.2 mm. long, 0.8–1.4 mm. wide, tips recurving at maturity, inner surface resinous, edges occasionally fimbriate, the outer phyllaries deltoid, 0.6–1.1 mm. long, 0.3–0.8 mm. wide; pappus light brown, the inner bristles 4.5–5.5 mm. long, the outer pappus of fimbriate scales, 1–1.2 mm. long; corollas 6–7.2 mm. long, bright purple, some with resin dots at tips of petals; anthers 2.3–2.9 mm. long. Achenes ca. 2 mm. long, sericeous, ribbed. Chromosome number $n = 17$. Flowering and fruiting from December to March.

DISTRIBUTION. Steep, eroded limestone hills in the Cockpit Country of Jamaica, between 300 and 900 meters, restricted to two locations (MAP 1).

REPRESENTATIVE SPECIMENS. **Jamaica.** ST. JAMES PARISH: Glencoe district, 1 mi. SE. of Stonehenge, *Proctor 24717* (GH); type locality, White Rock Hill, ca. 1 mi. S. of Sweetwater, *Keeley & Keeley 1247–1267* (GA).

This species has a distinctive habit, with an almost vinelike appearance and whorled leaves. Its restricted distribution and unusual morphology suggest that it has diverged from the main line of evolution of ARBORESCENTES in the West Indies. *Vernonia verticillata* also has an unusual spineless pollen grain (Keeley & Jones, 1977a).

4. **Vernonia rigida** (Swartz) Swartz, Fl. Ind. Occ. 3: 1322. 1806.

Conyza rigida Swartz, Prodr. 113. 1788. TYPE: Jamaica, *Swartz s.n.* (lectotype (here designated), s!; isotypes, BM!, s!).

Shrub, 1.5–2 meters high; stems ribbed and covered with downy, golden brown tomentum. Leaves sparse except at tips of branches; petioles 4–7 mm. long, with dense, golden brown pubescence; blades 3–5 cm. long, 2–3.5 cm. wide, length/width ratio ca. 1.5, widest at or below the middle, ovate to round-deltoid, coriaceous, shiny, gland dotted and with occasional short hairs above, resinous and more pubescent below, apex blunt to obcordate, base rounded to truncate, margins densely white-tomentose, entire. Inflorescences of rigid, extended cymes; heads (13- to) 20- to 25-flowered, sessile; involucres turbinate to deeply campanulate, 10–15 mm. high, 6–7 mm. wide, the phyllaries shiny, resinous, and with scattered pubescence, tightly appressed, imbricate in many spiral series, golden brown, often with dark tips, the inner phyllaries lanceolate, 5.7–7 mm. long, 1.3–1.5 mm. wide, with tips acuminate, recurved on some, the outer phyllaries deltoid, 0.9–1.5 mm. long, 0.4–1 mm. wide; pappus brown, the inner bristles 4–6.5 mm. long, the outer pappus of fimbriate scales, 0.8–1.5 mm. long; corollas ca. 9 mm. long, bright rose-purple, glabrous or rarely resin dotted at base; anthers ca. 3 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed. Chromosome number $n = 17$. Flowering and fruiting from December to March.

DISTRIBUTION. Eroded limestone cliffs and hillsides near the Cockpit Country, Jamaica, between 400 and 600 meters (MAP 2).

REPRESENTATIVE SPECIMEN. **Jamaica.** CLARENDON PARISH: Quaco Rock, above Ritches, *Keeley & Keeley 1186* (GA).

This species, with its thick stems and large heads, is distinctive. It is included here in subsection ARBORESCENTES because of the characteristics of its flowers and achenes; however, it is possible that it may actually represent a separate subsection. The shape of the involucres and the number of phyllaries is unusual, but several Cuban species share these traits and are otherwise typical ARBORESCENTES taxa. *Vernonia rigida* also has an atypical spineless pollen grain; its nearest analogue is found in *V. pineticola* of Cuba (Keeley & Jones, 1977a).

Swartz's description of *Conyza rigida* refers to Plumier's *Plantarum Americanarum* 4: *t. 14, fig. 1.* There is no illustration of a *Conyza* or even of a Composite in this work, however. Fournier (1932) reported that Plumier's drawings, recopied and edited in this volume by J. Burmann, contained many errors and misplaced parts, and the protologue to which Swartz referred is no longer available. Since Swartz collected genuine *Vernonia rigida* in Jamaica and described it accurately, it seems reasonable to choose a lectotype from among his collections.

5. **Vernonia segregata** Gleason, Bull. Torrey Bot. Club 40: 327, 328. 1913. TYPE: Cuba. Oriente Prov., vicinity of Camp San Benito, 24 Feb. 1910, *Shafer 4050* (holotype, NY!).

Shrub, ca. 1 meter high; stems closely pubescent, ribbed. Leaves evenly distributed along main stems; petioles 1–2 mm. long, densely pubescent; blades 1.7–4.9 mm. long, 1–2.4 mm. wide, length/width ratio ca. 1.5, widest at or slightly above the middle, oblong to oblong-elliptic, resinous, punctate and with occasional hairs above, pubescent and with prominent veins below, the apex acute, more rarely acuminate, the base rounded to cuneate to cordate, the margins entire or remotely denticulate on upper third, occasionally revolute. Inflorescences of condensed divaricate cymes, appearing as capitate clusters; heads 5- to 7-flowered, sessile; involucres campanulate, 3.5–5 mm. high, 3.5–6 mm. wide, the phyllaries thinly covered with white hairs, longest at the margins, loosely appressed, golden, the inner phyllaries linear to oblong, (3.5–)4–4.8 mm. long, 1.3–2 mm. wide, with tips tapering, but sharp, the outer phyllaries triangular to lanceolate, 1.4–2 mm. long, 0.4–0.8 mm. wide; pappus white to pale straw colored, the inner bristles 4 mm. long, the outer pappus of fimbriate scales, ca. 1 mm. long; corollas 5–6 mm. long, white to purple, glabrous; anthers 2–3 mm. long. Achenes 1.5–2.5 mm. long, sericeous to sparsely hirsute, ribbed. Flowering and fruiting throughout the year.

DISTRIBUTION. Between 500 and 600 meters, in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: on the road from Navas to Sierra de Buena Vista, *Ekman 3876* (S); Camp La Gloria, S. of Sierra Moa, *Shafer 8216* (F, NY); Taco Bay, on the ridge between Santa Maria and Jiquani rivers, *Ekman 3776* (GH, MO, NY).

This species is very poorly represented in collections. It recalls *Vernonia pluvialis* of Jamaica, to which it may be related. Field work in Cuba with this species would be helpful in resolving relationships with other species, as well as in affirming the validity of this taxon.

6. **Vernonia pluvialis** Gleason, Bull. Torrey Bot. Club **40**: 312. 1913. TYPE: Jamaica. St. Thomas Parish, Blue Mt. Peak, 14 May 1906, *Shreve s.n.* (holotype, NY!).

Vernonia proclivis Gleason, *ibid.* 312, 313. TYPE: Jamaica. St. Andrew Parish, vicinity of Cinchona, 2–10 Sept. 1906, *Britton 102* (holotype, NY!).

Vernonia reducta Gleason, *ibid.* 313, 314. TYPE: Jamaica. St. Andrew Parish, vicinity of Cinchona, 2–10 Sept. 1906, *Britton 203* (holotype, NY!).

Vernonia pluvialis Gleason var. *reducta* Fawcett & Rendle, Fl. Jam. **7**: 161. 1936.

Shrub, 1–2 meters high; stems sparsely pubescent, ribbed. Leaves evenly spread along main stems, generally all of similar size, sessile or with strigose to villous petioles to 5 mm. long; blades 3.5–7.5 cm. long, 0.9–2.5 cm. wide, length/width ratio ca. 3, widest at or just above the middle, elliptic to lanceolate, rugose, sparsely gland dotted and with scattered thin pubescence above, gland dotted and with prominent veins below, apex acute to acuminate, base cuneate, the margins entire to serrate, occasionally revolute. Inflorescences of compact divaricate cymes, often much condensed on terminal branches; heads 5- to 7-flowered, sessile, variably pubescent; involucres campanulate, sometimes appearing constricted at the top, 4–6 mm. high, 3–4 mm. wide, the phyllaries tomentose, tightly appressed, gold to brown, the inner phyllaries linear to oblong, sides often rolled inward creating a triangular phyllary, 4–5 mm. long, 0.8–1.4 mm. wide, tips acute, the outer phyllaries elliptic, 0.9–1.5 mm. long, 0.3–0.7 mm. wide; pappus brown, the inner bristles 4–5.5 mm. long, the outer pappus of fimbriate scales, 0.5–1 mm. long; corollas 5.5–7 mm. long, pink to white, with resinous dots; anthers 1.5–2 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed. Chromosome number $n = 17$. Flowering and fruiting from October to July.

DISTRIBUTION. Moist woods, along paths through rain forest areas and on mountain tops, in the Blue Mountains, Jamaica, between 1500 and 2500 meters (MAP 1).

REPRESENTATIVE SPECIMENS. **Jamaica.** PORTLAND PARISH: upper E. ridge and summit, Mossman's Pk., *Maxon 9690* (GH, US). ST. THOMAS PARISH: Blue Mts., montane rainforest between Portland Gap and Blue Mt. Pk., *Webster 5446* (GH, US); head of Mabess River, Blue Mts., *Philipson 865* (F, NY).

This species is characteristic of the highest peaks in Jamaica and can be found in abundance along trails and in clearings. It is extremely polymorphic, but collections from within a small area encompass the variations recognized as distinct species by Gleason (1906). It is low growing and often forms small thickets and hedges.

7. **Vernonia albicaulis** Persoon, Syn. Pl. 2: 404. 1807.

Synonymies and typifications are given under the subspecific headings.

Shrub, 0.5–2.5 meters high; stems generally woody, pilose to hispid, gland dotted, occasionally gray- or black-speckled, usually ribbed. Leaves evenly dispersed along main stems and branches, typically more crowded on terminal branchlets; petioles 1–11 mm. long, pubescent; blades 2–15 cm. long, 0.8–5.6 cm. wide, length/width ratio ca. 2, widest at or slightly above the middle, oblong to elliptic, sparsely pilose-hispid to glabrate and gland dotted above, sparsely strigose below, the apex acute to obtuse, occasionally obcordate, the base cuneate to tapering, the margins entire to repand. Inflorescences cymose to rarely subcorymbose and much condensed; heads (10- to) 11- to 20- (to 23-)flowered, sessile or with peduncles to 1 mm. long and pubescent as on leaf surfaces; involucre campanulate, 4–6 mm. high, 4–7 mm. wide, the phyllaries pilose to hispid, pubescence decreasing with age, occasionally gland dotted, imbricate in few series, firmly appressed until maturity, golden brown with brown tips, the inner phyllaries linear to elliptic, 3.5–5 mm. long, 0.6–1 mm. wide, with tips acute, sometimes recurved, the outer phyllaries awl shaped to deltoid, 0.8–1.3 mm. long, 0.3–0.8 mm. wide; pappus pale brown to rarely white, the inner bristles 4–6 mm. long, the outer pappus of fimbriate scales, 0.5–1 mm. long; corollas 5–10 mm. long, lavender, pink, or white, glabrous; anthers 2–3.5 mm. long. Achenes ca. 3 mm. long, ribbed, hispid to sericeous, occasionally resin dotted. Chromosome number $n = 17$. Flowering and fruiting throughout the year.

Two subspecies of *Vernonia albicaulis* are recognized. Their distributions are shown in MAP 2. They are characterized and distinguished by the following key:

Pappus brown; styles 6–10 mm. long. ..... 7a. subsp. *albicaulis*.
Pappus white or slightly dirty white; styles 12–25 mm. long. .....
..... 7b. subsp. *longistylis*.

7a. **Vernonia albicaulis** Persoon subsp. **albicaulis**. TYPE: St. Crucis [St. Croix], *Vahl 737* (holotype, P-JU (IDC B–6206–2. 621: I. 4!)).

Conyza glabra Willdenow, Sp. Pl. 3: 1940, 1941. 1803. TYPE: America Meridionali [Central America], *Vahl s.n.* (Herb. Willd. #15622) (lectotype (here designated) B, as photo B!).

Eupatorium obtusifolium Willdenow, *ibid.* 1768. TYPE: America Calidiore

[Central America], *Vahl s.n.* (Herb. Willd. #15144) (lectotype (here designated) B, as photo B!).

Vernonia longifolia Persoon, Syn. Pl. **2:** 404. 1807. TYPE: St. Crucis (St. Croix), *Vahl 737* (holotype, P-JU (IDC B–6206–2. 621: I. 4!)).

Lepidaploa albicaulis (Persoon) Cassini, Dict. Sci. Nat. **26:** 17, 18. 1823.

Ledidaploa lanceolata Cassini, *ibid.* 18. TYPE: *Desfontaines s.n.* (holotype, FI).

Vernonia punctata Swartz ex Wikström, Sv. Vet.-Akad. Handl. **1827:** 72, 73. 1828. TYPE: Guadeloupe. *Forsstrom s.n.* (lectotype (here designated), S!).

Vernonia emarginata Wikström, *ibid.* 73. TYPE: Guadeloupe, *Forsstrom s.n.* (lectotype (here designated), S!).

Vernonia vahliana Lessing, Linnaea **4:** 306–308. 1829. TYPE: America Meridionali [Central America], *Vahl s.n.* (Herb. Willdenow #15622) (lectotype (here designated) B, as photo B!).

Eupatorium secundiflorum Bertero ex de Candolle, Prodr. **5:** 48. 1836, p.p. TYPE: Guadeloupe, 1821, *Balbis 44* (holotype, G-DC (IDC B–800–2. 773: II. 3!)).

Vernonia arborescens β ovatifolia de Candolle, *ibid.*, p.p. TYPE: Cuba. La Havane, 1825, *de la Ossa s.n.* (holotype, G-DC (IDC B–800–2. 773: II. 3!)).

Vernonia thomae Bentham, Vidensk. Medd. Naturh. For. Kjøbenhavn **5–7:** 66. 1852. TYPE: St. Thomas. Hillside thicket, Water Island, 31 Jan.–4 Feb. 1913, *Britton, Britton, & Shafer 142* (isoneotypes (here designated), NY!, US!). No specimen cited as type or found at K or BM; it is presumed to have been lost or destroyed.

Cacalia punctata (Swartz ex Wikström) Kuntze, Rev. Gen. Pl. **2:** 970. 1891.

Cacalia thomae (Bentham) Kuntze, *ibid.* **1:** 324.

Vernonia longifolia α genuina Urban, Symb. Antill. **1:** 456. 1899. TYPE: Guadeloupe. Basse Terre, Vieux Fort, 1893, *Duss 2489* (isolectotypes (here designated), GH!, NY!).

Vernonia longifolia β sintenisii Urban, *ibid.* TYPE: Puerto Rico. Mayaguez Prov., in declivibus montis vi, inter filices, 8 July 1886, *Sintenis 4371* (lectotype (here designated), GH!).

Vernonia longifolia γ vahliana (Lessing) Urban, *ibid.* 456, 457. TYPE: America Meridionali [Central America], *Vahl s.n.* (Herb. Willdenow #15622) (lectotype (here designated), B, as photo B!).

Vernonia sintenisii (Urban) Gleason, Bull. N. Y. Bot. Gard. **4:** 187. 1906.

Vernonia Gleasonii Ekman, Ark. Bot. **13:** 54, 55. 1914. TYPE: Puerto Rico. Mayaguez Prov., in declivibus montis Llano, 6 July 1886, *Sintenis 4749* (isolectotypes (here designated), F!, GH!, MO!, NY!, S!).

Vernonia shaferi Gleason, Bull. Torrey Bot. Club **46:** 238, 239. 1919. TYPE: Montserrat. Gages, below Soufrière, 20 Jan. 1907, *Shafer 172* (holotype, NY!; isotypes, GH!, US!).

DISTRIBUTION. Limestone cliffs and hillsides, 150 to 250 (to 600) meters, Puerto Rico and the Lesser Antilles, as shown in MAP 2.

REPRESENTATIVE SPECIMENS. **Anguilla:** N. of the Valley, *Proctor 18543* (US). **Antigua:** *Rose, Fitch, & Russell 3291* (F, US). **Dominica:** "Sylvania," *Cooper 88* (F, GH, NY, US). **Great Camanoe:** near top of South Hill, *D'Arcy 799* (GH). **Guadeloupe:** Vieux Habitantes, *Questal 4529* (US). **Montserrat:** gorge of river leading from the Soufrière, *Shafer 589* (NY, US). **Puerto Rico:** Guayanilla to

Tallahoa, rocky coastal thicket, *Shafer 1999* (F, NY, US). **St. Barthélemy:** Morne Grand Ford, *Questel 112* (US). **St. Croix:** roadside near East End, *Ricksecker 220* (F, GH, MO, NY, US). **Santa Cruz:** *Canby s.n.* (NY). **St. Kitts:** banks of gulch near Old Road, *Britton & Cowell 144* (NY). **St. John:** vicinity of Caneel Bay, *Woodworth 78* (F). **St. Maarten:** hills along northern side of Cul de Sac, *Stoffers 2635* (GH). **St. Thomas:** Water Is., *Britton, Britton, & Shafer 142* (F, NY, US). **Virgin Gorda:** summit & eastern slope of Virgin Pk., *Smith 10566* (GH, NY, S, US).

This is the most common species of coastal areas of Puerto Rico and the Lesser Antilles. It is often found on rocky cliffs and is visible at a distance due to the dense clusters of flowers. It is occasionally cultivated.

There was some confusion in the Willdenow herbarium surrounding the types of *Conyza glabra* and *Eupatorium obtusifolium* (H. W. Lack, pers. comm.). Labels on the covers of the folders disagree in part with the description of these two species. It is not clear which, if either, of these sheets represents the holotype of *C. glabra* or *E. obtusifolium*. Sheet #15144, labeled *Eupatorium obtusifolium*, was chosen as the lectotype for this species; sheet #15622, labeled *Conyza glabra*, was selected for this species.

Ekman (1914) described a hybrid between *Vernonia albicaulis* and *V. sericea* and published it above a new name, *V. gleasonii*, in his revision. Since he did not place *Vernonia gleasonii* in a prominent position, but rather published the two species names first, with an × between them to indicate the hybrid nature of this "taxon," I do not believe that he actually wished to recognize a new species. I have placed the name in synonymy on this basis, and also because the specimens cited are well within the normal range of variation in *Vernonia albicaulis* and are not indisputably hybrid in origin. *Vernonia albicaulis* typically grows near the coast and at relatively low elevations in Puerto Rico, whereas *V. sericea* is found in the center of the island, above 300 meters; the hybrids between these species must be a great rarity if they occur at all in nature.

7b. **Vernonia albicaulis** subsp. **longistylis** Keeley, subsp. nov.

Corolla 9–10 mm. longa; antherae 3–3.5 mm. longae; stylus exertus 10–20 mm. longus. Pappi setae albae, eis interioribus 5.5–6 mm. longis, eis externis 1–1.2 mm. longis.

TYPE: Guadeloupe. Basse Terre, limestone cliffs along roadside, facing inland, 2 km. W. of Pt. de la Saline, along hwy. to St. Ann, 20 Dec. 1975, *Keeley & Keeley 1948a* (holotype, GA!).

DISTRIBUTION. This subspecies is known only from Guadeloupe and the small islands near it, Isles des Saintes and Marie-Galante. It is somewhat taller and more robust than the typical subspecies and can easily be recognized by its white pappus and prominent styles. It is found on limestone and volcanic soils between 150 and 240 meters.

REPRESENTATIVE SPECIMENS. **Guadeloupe.** BASSE TERRE: Road to Vieux Fort

past Grande Anse beach, on steep volcanic banks, *Keeley 1975* (GA). GRANDE TERRE: vicinity of Anse Patate, *Proctor 19926* (GH, US); vertical limestone cliffs, 1 km. W. of Fonds-Thézan, *Keeley & Keeley 1993* (GA).

8. Vernonia sericea Richard, Actes Soc. Hist. Nat. Paris 1: 112. 1792. TYPE: Puerto Rico, *Baudin 292* (lectotype (here designated), P-JU (IDC B–6206–2. 620: III. 7!)).

Lepidaploa phyllostachya Cassini, Dict. Sci. Nat. **26:** 16, 17. 1823. TYPE: Puerto Rico, *Baudin 292* (lectotype (here designated), P-JU (IDC B–6206–2. 620: III. 7!)).

Vernonia Berteriana de Candolle, Prodr. **5:** 52. 1836. TYPE: Puerto Rico, 1820, *Bertero & Balbis s.n.* (holotype, G-DC (IDC B–800–2. 774: I. 3!)).

Conyza portoriccensis Bertero ex de Candolle, *ibid.* TYPE: Puerto Rico, 1820, *Bertero & Balbis s.n.* (holotype, G-DC (IDC B–800–2. 744: I. 3!)).

Vernonia racemosa Delponte, Mem. Reale Accad. Sci. Torino. ser. 2. **14:** 396–398. 1854. TYPE: *op. cit. pl. II*, p. 398, with analyses.

Vernonia arborescens β Lessingiana Grisebach, Fl. Brit. W. Indian Is. 353. 1861, p.p. TYPE: Puerto Rico. Based on C. Plumier (ed. J. Burmann), Pl. Amer. 122. *t. 130, fig. 2.* 1757.

Vernonia remotiflora Richard forma *angustifolia* Grisebach, Cat. Pl. Cubens. 144. 1866, p.p. TYPE: Cuba, 1860, *Wright 2786* (holotype, K!; isotype, GH!).

Vernonia stenophylla Gleason, Bull. N. Y. Bot. Gard. **4:** 181. 1906. TYPE: Cuba, 1860, *Wright 2786* (holotype, GH!; isotype, K!).

Vernonia phyllostachya (Cassini) Gleason, *ibid.* 176, 177.

Vernonia venusta Gleason, *ibid.* 177. TYPE: Puerto Rico. Ponce Prov., on the Adjuntas rd., 7 mi. from Ponce, 27 Nov. 1902, *Heller 6136* (holotype, NY!; isotypes, F!, US!).

Vernonia araripensis sensu Gleason, *ibid.* 181, non *V. araripensis* Gardner, 1846.

Vernonia angustissima Wright ex Ekman, Ark. Bot. **13:** 78, 80. 1914. TYPE: Cuba, 1860, *Wright 2786* (holotype, K!; isotype, GH!).

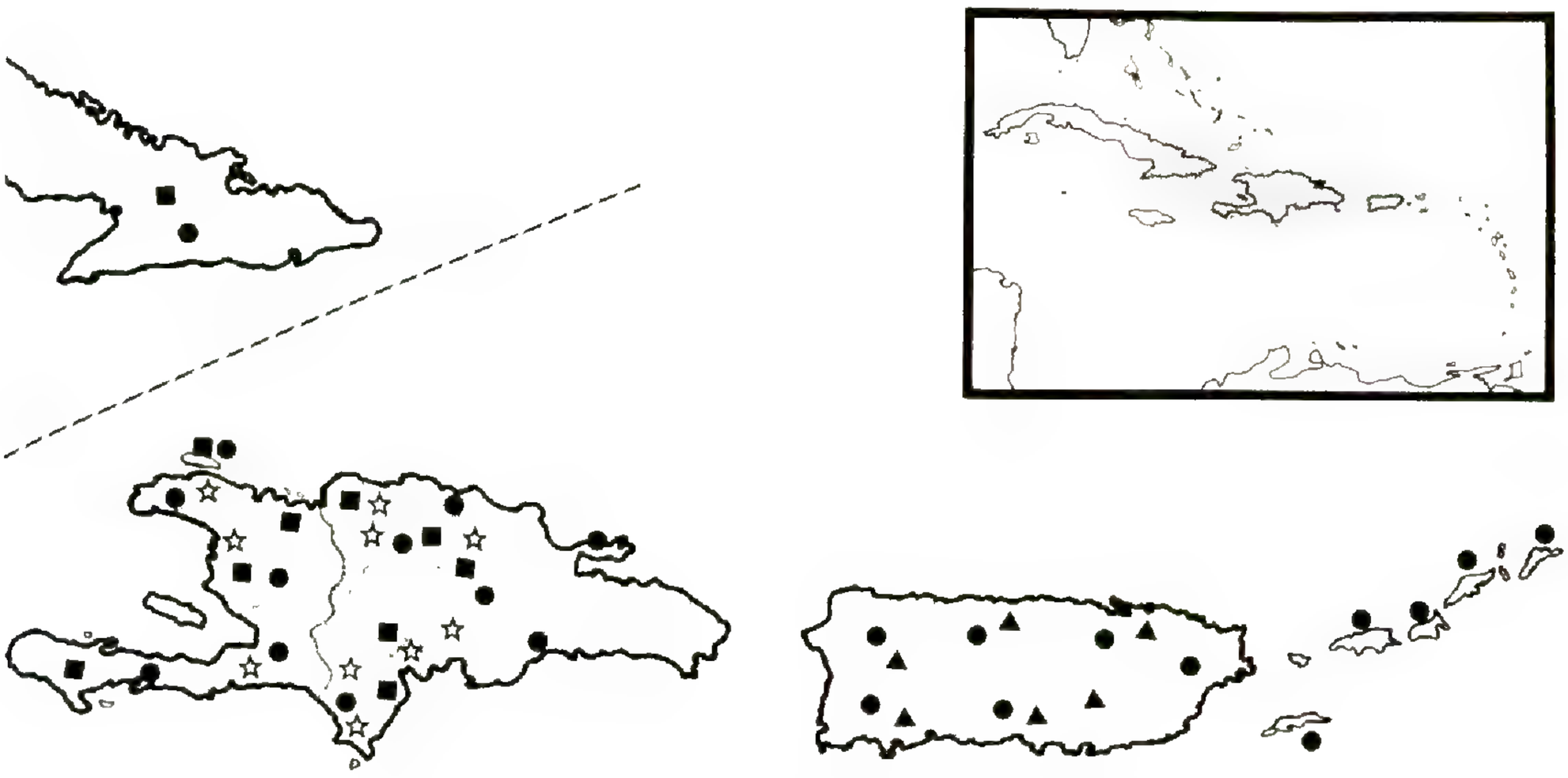
Vernonia sericea Richard subsp. *racemosa* (Delponte) Ekman, *ibid.* 85, 86.

Vernonia racemosa sensu Gleason, N. Am. Fl. **33:** 64, 65. 1922, non *V. racemosa* Delponte, 1854.

Vernonia maestralis Ekman ex Urban, Repert. Sp. Nov. **26:** 99. 1929. TYPE: Cuba. Oriente Prov., Sierra Maestra, La Bayamesa, on the ridge between Gro and Río Yao, 5 May 1916, *Ekman 7211* (holotype, S!; isotypes, F!, NY!, S!).

Vernonia sericea Richard subsp. *racemosa* var. *angustifolia* (Delponte) Ekman, Ark. Bot. **23A:** 48, 49. 1930. TYPE: Haiti. Départ de Sud-Ouest, Massif de la Selle, Pétionville, Chapi Faure, 27 Aug. 1924, *Ekman 1653* (holotype, S!; isotype, US!).

Shrub, 1–1.5 meters high; stems pubescent, becoming glabrate with age, gray to brown, ribbed. Leaves often crowded at nodes, sometimes fasciculate; petioles 1–5 mm. long, pubescent; blades 3.5–10 cm. long, 0.2–2.5 cm. wide, length/width ratio variable, widest at or slightly below the middle, elliptic, lanceolate to linear, pilose-hispid to strigose and with few glands above, sericeous and with brownish, protruding veins below, apex



MAP 3. Distribution of *Vernonia borinquensis* (triangles), *V. sericea* (circles), *V. stenophylla* (squares), and *V. fruticosa* (stars) in Oriente Province, Cuba, Haiti and the Dominican Republic, Puerto Rico, and the Virgin Islands.

acute to rarely acuminate, base tapering to cuneate, the margins entire, often revolute. Inflorescences of scorpioid cymes, variably extended; heads 11- to 15- (to 18-)flowered, sessile; involucres campanulate, 5–6 mm. high, 5–8 mm. wide, the phyllaries strigose to villous, pubescence thinning at maturity, loosely appressed, tan to golden colored, some with dark tips, the inner phyllaries subulate to lanceolate, 4.6–6 mm. long, 0.8–1.1 mm. wide, tips acuminate to acute, the outer phyllaries lanceolate to elliptic, 1.5–2 mm. long, 0.3–0.5 mm. wide; pappus brown, the inner bristles (3.5–)4–4.5 mm. long, the outer pappus of fimbriate scales, 0.3–0.7 mm. long; corollas (4.5–)5–6 mm. long, lavender to white, glabrous; anthers 0.8–1.5 mm. long. Achenes ca. 2 mm. long, sericeous, ribbed. Chromosome number $n = 17$. Flowering and fruiting throughout the year.

DISTRIBUTION. Mountains, pine forests, on limestone and in moist areas, between 325 and 1600 meters, in Puerto Rico, the Virgin Islands, Hispaniola, and in Oriente Province, Cuba (MAP 3).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Sierra de Nipe, near Woodfred, *Shafer 3552* (F, NY, S). **Dominican Republic.** DISTRITO NATIONAL: Llano Costero at San Carlos, *Ekman 11393* (F, GH, NY, US). LA VEGA PROV.: slopes along hwy. between Constanza and Valle Nuevo, *Allard 17433* (NY, S, US). PEDERNALES PROV.: Agua Negra, Sierra del Bahoruco, *Liogier 13955* (GH, NY). PUERTA PLATA PROV.: El Choco, *Jiménez 4374* (US). SAMANA PROV.: Peninsula de Samana, Boca Río San Juan, *Ekman 15006* (US). SANTIAGO PROV.: Pastor, *Jiménez 1794* (GH, US). **Haiti.** DÉPART DE L'ARTIBONITE: SE. of Ennery, *Leonard 8990* (US). DÉPART DU NORD-OUEST: Montagnes de Terre Neuve, Les Gonaiives Même, *Ekman 9464* (F, NY, TEX, US). DÉPART DU SUD: prope Civette, *Ekman 222* (US). DÉPART DU SUD-OUEST: along rd. E. of Plateau Pistache, Massif de La Selle, *Proctor 10768* (US). ÎLE DE LA TORTUE: E. of La Vallée, *Leonard & Leonard 11382* (US); Morne des Commissaires, *Holdridge 1310* (GH, NY). **Puerto Rico.** AGUADILLA PROV.: Lares, *Britton, Britton, & Hess 2747* (NY, US). SAN

JUAN PROV.: Río Piedra, Bo. Guadalcanal, Distr. Bayamon, *Otero 417* (GH, MO). HUMACAO PROV.: Luquillo, Bo. Pitajaya, Distr. Bayamon, *Otero 519* (F, GH, MO). MAYAGUEZ PROV.: 14 mi. NE. of Mayaguez, *Heller 4472* (F, NY, US). PONCE PROV.: Ponce to Peñuelas, *Britton, Britton, & Marble 1781* (F, NY). VIEQUES Is.: Cerro Ventana, *Shafer 2867* (GH, NY). **Virgin Islands.** VIRGIN GORDA: thickets on mt., *Fishlock 102* (NY). ST. THOMAS: Charlotte Amalie, *Armour 551* (F, NY). TORTOLA: hillside, high bush, *Britton & Shafer 818* (NY). ST. JAN [St. John]: Roseberg, *Britton & Shafer 303* (NY, US).

The variation in leaf size has been reflected in several infraspecific designations in past treatments. There is no justification for the maintenance of these infraspecific taxa since both broad- and narrow-leaved forms occur in the same population and, on some occasions, on the same plant. This is an easily recognized species and can be found in forests and wet places in the mountains. The Cuban collections all appear to be narrow leaved, but collections are meager.

9. **Vernonia borinquensis** Urban, Symb. Antill. 3: 390, 391. 1903. TYPE: Puerto Rico. Arecibo Prov., Maricao in sylvis, 12 Nov. 1884, *Sintenis 388* (isolectotypes (here designated), NY!, S!).

Vernonia borinquensis var. *stahlii* Urban, *ibid.* 391. TYPE: Puerto Rico. San Juan Prov., Bayamon, *Stahl 667* (lectotype (here designated), S!).

Vernonia borinquensis var. *resinosa* Gleason, Bull. Torrey Bot. Club **46**: 236. 1919. TYPE: Puerto Rico. Guayama Prov., Cayey, mt. slopes above the town, Jan. 1911, *Holway s.n.* (holotype, NY!).

Vernonia borinquensis var. *hirsuta* Gleason, *ibid.* TYPE: Puerto Rico. Mayaguez Prov., Río de Maricao, wooded valley, 2 April 1913, *Britton, Stevens, & Hess 2471* (holotype, NY!; isotype, US!).

Shrub, often sprawling, 0.5–3 meters tall; stems densely gray-white-pubescent, ribbed. Leaves evenly spaced along main stems and below heads; petioles 1–4 mm. long, densely pubescent; blades 2–4.7 cm. long, 0.7–2.5 cm. wide, length/width ratio ca. 2, widest at or just below the middle, lanceolate to ovate, gland dotted, shiny, often rugose or pustulate-pubescent above, often similar below, but may be covered with velutinous tomentum, most pubescence along veins, the apex acute, tapering to arcuate, the base tapering, occasionally oblique, the margins entire or minutely denticulate, often revolute. Inflorescences of conspicuous stiff, zigzag cymes; flower heads large and showy, (13- to) 16- to 22-flowered, sessile; involucres campanulate, 5.5–8 mm. high, 7–11 mm. wide, the phyllaries densely pubescent to barely so, loosely appressed in mature heads, green to golden brown, the inner phyllaries awl shaped to lanceolate, (5.2–)6–7.5 mm. long, 0.8–1.4 mm. wide, with tips long-tapering, acute, the outer phyllaries lanceolate, tapering, 1–2.4 mm. long, 0.4–0.7 mm. wide; pappus brown, the inner bristles 5–6.5 mm. long, the outer pappus of fimbriate scales, 0.5–1 mm. long; corollas 6–8 mm. long, white or lavender, glabrous, sometimes with resinous dots at tips of petals, no conspicuous odor;

anthers 2.5–3.3 mm. long. Achenes 1–2 mm. long, ribbed, sericeous. Chromosome number $n = 17$. Flowering and fruiting throughout the year.

DISTRIBUTION. Steep, moist banks of clay, limestone, or serpentine, between 300 and 1200 meters, in Puerto Rico (MAP 3).

REPRESENTATIVE SPECIMENS. **Puerto Rico.** AGUADILLA PROV.: Guavate State Forest, *Liogier 10354* (NY, US). ARECIBO PROV.: roadside bank, vicinity of Utuado, *Britton 5202* (NY, US). GAYAMA PROV.: 2 km. W. of Aibonito, *Howard & Nevling 15336* (GH). MAYAGUEZ PROV.: in woods, Las Mesas, *Liogier 10528* (F, GH, NY, US). PONCE PROV.: moist bank, vicinity of Ala de la Piedra, above Villalba, *Britton & Earl 6091* (NY, US).

This species can be easily recognized by its large heads and zigzag cymes. It is rather variable with respect to pubescence, accounting in part for the several varieties that have previously been recognized. Greenhouse-grown accessions show variable amounts of pubescence with age, and there seems little reason for maintaining subspecific status based on this trait.

10. **Vernonia divaricata** Swartz, Fl. Ind. Occ. 3: 1319. 1806. TYPE: Jamaica, *Swartz s.n.* (holotype, s!; isotype, s!).

Vernonia arborescens Swartz γ *divaricata* Grisebach, Fl. Brit. W. Indian Is. 353. 1861, p.p.
Vernonia acuminata sensu Grisebach, *ibid.*, non *V. acuminata* Lessing, 1829.
Vernonia gnaphalifolia sensu Grisebach, Cat. Pl. Cubens. 144. 1886, p.p., non *V. gnaphaliifolia* Richard, 1850.
Vernonia albicoma Gleason, Bull. N. Y. Bot. Gard. **4:** 185, 186. 1906. TYPE: Jamaica. West of Long Mt., 13 Jan. 1896, *Campbell 6152* (holotype, NY!).
Vernonia intonsa Gleason, *ibid.* 182. TYPE: Jamaica. Arnold Rd., 25 Nov. 1895, *Campbell 6091* (holotype, NY!).
Vernonia amaranthina Gleason, Bull. Torrey Bot. Club **40:** 307, 308. 1913. TYPE: Jamaica. Hanover Parish, "Greenland" (Green Island), 13 March 1908, *Britton 2897* (holotype, NY!).
Vernonia permollis Gleason, Bull. N. Y. Bot. Gard. **4:** 181, 182. 1906. TYPE: Jamaica. St. Andrew Parish, Cinchona, May 1903, *Shreve s.n.* (holotype, NY!).
Vernonia parvuliceps Ekman, Ark. Bot. **13:** 71, 72. 1914. TYPE: Cuba. Oriente Prov., Pinar de S. J. de Buenamito, 18 Nov. 1860–64, *Wright 2788* (holotype, K!; isotype, GH!).

Shrub, 1–3 meters high; stems tomentose, ribbed. Leaves uncrowded, subbracteal leaves resembling the cauline, but smaller; petioles 4–8 mm. long, tomentose; blades (3.8–)4–9 cm. long, 2–4.2 cm. wide, length/width ratio ca. 2, widest at or below the middle, ovate to broadly lanceolate, rugose, occasionally bullate, shiny dark green surface, covered by numerous hairs above, densely tomentose, often velvety below, apex acute to acuminate, with tip slightly curved, base rounded to truncate, margins entire. Inflorescences of scorpioid cymes, subbracteal leaves reduced or occasionally lacking; heads 12- to 20-flowered, sessile or with

hirsute to woolly-pubescent peduncles to 3 mm. long; involucres campanulate, 4–6 mm. high, 4–6 mm. wide, the phyllaries hirsute to villous, loosely appressed at maturity, often with recurving tips, straw colored to greenish, tips often purple, the inner phyllaries oblong to near top, then sharply acute, 4–5 mm. long, 0.8–1.4 mm. wide, with tips acute, often recurved, the outer phyllaries ovate, 0.8–1.6 mm. long, 0.3–0.7 mm. wide; pappus straw colored to clear white, the inner bristles 4–5 mm. long, the outer pappus of fimbriate scales, 0.5–1 mm. long; corollas 5.5–7 mm. long, lavender, white, or rarely pink, occasionally resin dotted at tips of petals; anthers 1.5–2.2 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed. Chromosome number $n = 17$. Flowering and fruiting throughout the year, but most conspicuously from December to March.

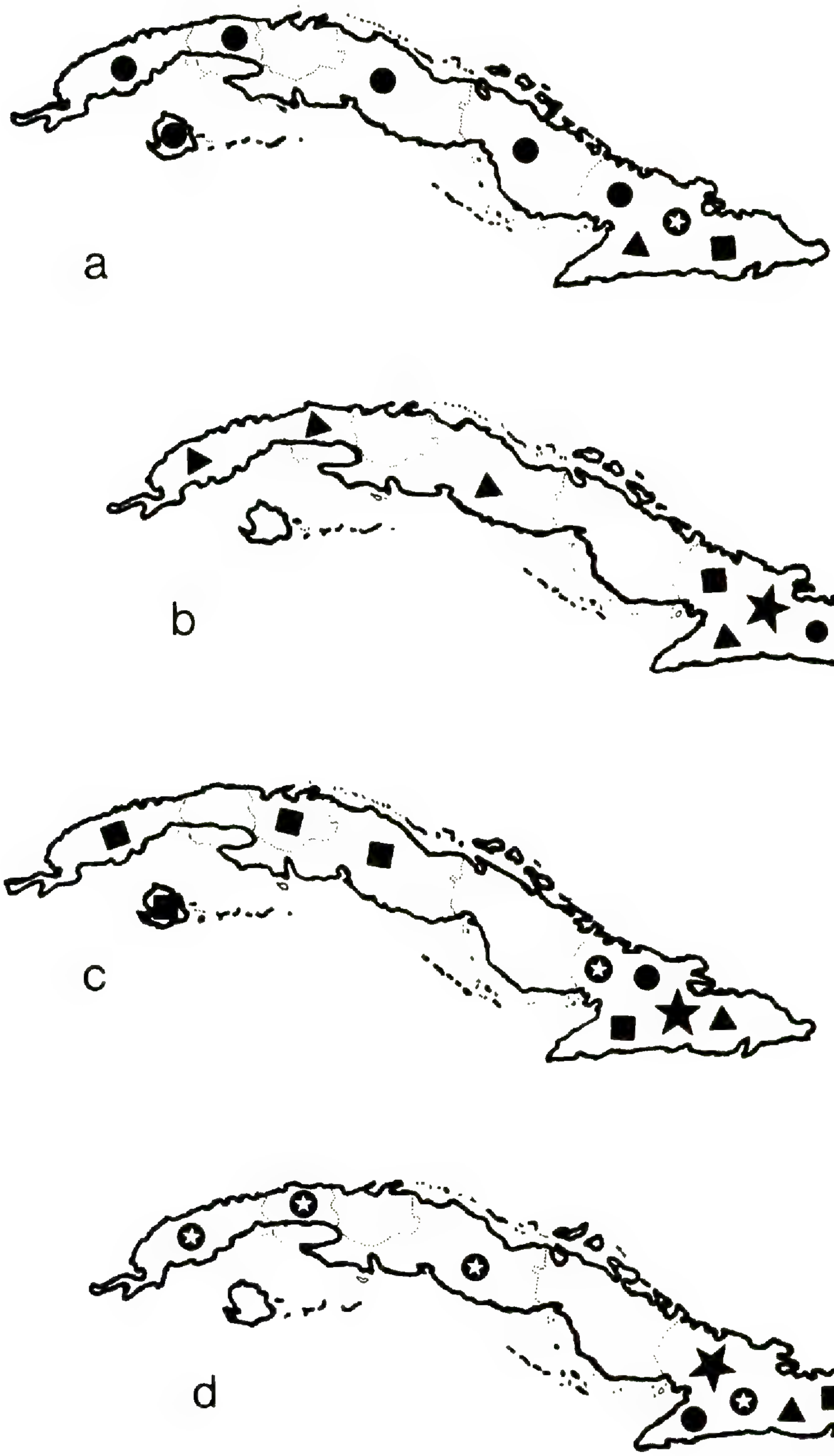
DISTRIBUTION. Moist slopes, in forests along roadsides and on limestone, serpentine, and clay soils, between 250 and 1800 meters, in Jamaica and Cuba (MAP 1).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Sierra Maestra, Loma Barbi, *Ekman 15651* (S); Sierra de Nipe, Loma la Cintura, near Piloto del Medio, *Ekman 10135* (GH, S, US). **Jamaica.** HANOVER PARISH: Quashiba Mt., ca. 1 mi. W. of George's Plain, *Webster & Wilson 5099* (GH). MANCHESTER PARISH: Martin's Hill, *Britton 3762* (NY). PORTLAND PARISH: Blue Mts., near Resource, *Perkins 1265* (GH). ST. ANDREW PARISH: Liguanea Ridge, *Harris 12207* (F, GH, MO, US). ST. ANN PARISH: on roadside below Union Hill, 2.5 mi. SSW. of Moneague, *Howard & Proctor 13605* (GH). ST. CATHERINE PARISH: ca. 1 mi. SW. of Parks Rd., *Webster & Wilson 5023* (GH). ST. ELIZABETH PARISH: gravelly hillside, Great Pedro Bay, *Britton 1259* (NY). ST. THOMAS PARISH: bushy hillside near Whitfield, *Proctor 6605* (NY, US). TRELAWNY PARISH: Miss Laura's Hill, Wilson Valley District, ca. 1 mi. N. of Warsop, *Proctor 31180* (TEX).

This species is the most commonly encountered *Vernonia* in Jamaica, but in Cuba it is known only from Oriente Province. Ekman (1914) described the Cuban population as *Vernonia parvuliceps*; however, there are no consistent differences to delimit the Cuban from the more abundant Jamaican plants. *Vernonia divaricata* has often been confused with *V. arborescens* in the past, largely due to Linnaeus's description that was based primarily on Plumier's figure, but secondarily modified using a Jamaican plant collected by Browne. For a more detailed discussion of this problem, see Ekman (1914). This species appears most similar to *Vernonia arborescens*, with which it has been confused, but is also similar to *V. leptoclada*, *V. sericea*, and *V. gnaphaliifolia*. The extent of relationships of these species to each other remains to be investigated.

11. **Vernonia arborescens** (Linnaeus) Swartz, Fl. Ind. Occ. 3: 1320. 1806.

Conyza arborescens Linnaeus, Syst. Nat. ed. 10. 2: 1213. 1759. TYPE: Martinique. Based on C. Plumier (ed. J. Burmann), Pl. Amer. 122. *t. 130, fig. 2.* 1757.



MAP 4. Distribution of *Vernonia* species in Cuba: a, *V. complicata* (square), *V. desiliens* (triangle), *V. divaricata* (circle with star in center), *V. gnaphaliifolia* (solid circles); b, *V. commutata* (square), *V. hieracioides* (circle with star in center), *V. jenssenii* (solid circle), *V. leptoclada* (star), *V. sagraeana* (triangles); c, *V. havanensis* (squares), *V. orbicularis* (triangle), *V. pineticola* (star), *V. purpurata* (circle with star in center), *V. segregata* (solid circle); d,

Lepidaploa arborescens Cassini ex Lessing, Linnaea **4:** 302. 1829.
Vernonia divaricata Lessing, *ibid.* 306. TYPE: Martinique, Sieber s.n. (Fl. Martinique #190) (holotype, L!; isotype, L!).
Vernonia arborescens β *ovatifolia* de Candolle, Prodr. **5:** 48. 1836, p.p. TYPE: Cuba(?). La Habana, 1825, *Ossa s.n.* (holotype, G-DC (IDC B–800–2. 773: II. 4!)).
Eupatorium secundiflorum Bertero ex de Candolle, *ibid.*, *pro. syn.*
Vernonia icosantha de Candolle, *ibid.* TYPE: Martinique, *Sieber s.n.* (Fl. Martinique #190) (holotype, L!; isotype, L!).
Vernonia arborescens Swartz β *Lessingiana* Grisebach, Fl. Brit. W. Indian Is. 353. 1864. TYPE: Martinique. Based on C. Plumier (ed. J. Burmann), Pl. Amer. 122. *t. 130, fig. 2.* 1757.
Cacalia arborescens (Linnaeus) Kuntze, Rev. Gen. Pl. **1:** 323, 324. 1891.
Vernonia ventosa Gleason, Bull. N. Y. Bot. Gard. **4:** 179. 1906. TYPE: Martinique, *"Duss 303, 304, 4069"* (holotype, NY!).

Shrub, 1–2 meters high; stems velvety-pubescent, ribbed beneath pubescence, and becoming glabrate with age, green to brown in color. Leaves generally spaced evenly, at least along the main stem, sometimes crowded on terminal branches and near heads; petioles 2–11 mm. long, pubescent; blades 4.5–11.3 cm. long, 1.3–4.5 cm. wide, length/width ratio ca. 3, widest below the middle, ovate-elliptic, gland dotted, villous to strigose, pubescence lessening above with age and expansion of the blade, hirsute-villous to sparsely hirsute and gland dotted, with prominent protruding veins below, the apex acuminate, sometimes acute, the base cuneate to rounded, the margins entire to repand. Inflorescences of scorpioid cymes, variable in length, occasionally condensed; heads 15- to 25- (to 29-)flowered, sessile; involucres campanulate, 4.5–6 mm. high, 5–9 mm. wide, the phyllaries hirsute, villous to nearly glabrous, imbricate, loosely appressed, reflexed in maturity, golden brown, the inner phyllaries linear-lanceolate, 4–6 mm. long, (0.8–)1–1.3 mm. wide, with tips acuminate, rarely mucronate, often with one strong central rib continuing into tip, the outer phyllaries subulate to linear, 1.3–2.5 mm. long, (0.3–)0.5–0.9 mm. wide; pappus white, the inner bristles 4–5 mm. long, the outer pappus of fimbriate scales, 0.7–1.2 mm. long; corollas 6–8 mm. long, lavender to white, resinous at tips of petals, rarely with faint sweet odor; anthers (2.2–)2.5–3 mm. long. Achenes 1.5–2 mm. long, sericeous, ribbed. Chromosome number $n = 17$. Flowering and fruiting throughout the year, but chiefly from December to May.

DISTRIBUTION. Volcanic soils along roadsides or rarely in thickets, from 50 to 300 meters, in Martinique and its immediate satellite islands, and St. Lucia and St. Vincent (MAP 2).

REPRESENTATIVE SPECIMENS. **Martinique:** Hauteurs de Case-Pilote, *Duss 984* (NY); Morne Vert region, *Webster, Ellis, & Miller 9206* (F, GH, US). **St. Lucia:**

V. aronifolia (solid circle), *V. menthaefolia* (circles with stars in centers), *V. urbaniana* (square), *V. wrightii* (star), *V. yunquensis* (triangle). *Vernonia viminalis* is not included since no distribution is known other than in Cuba.

Anse-la-Raye, *Beard 1099* (GH, MO, S, US). **St. Vincent:** Montrose Hills, *Eggers 6545* (GH, US).

Vernonia arborescens has been among the most confused and poorly understood of all West Indian species. It is typical of the ARBORESCENTES subsection and is undoubtedly closely related to several of the other species in this subsection, particularly to *V. divaricata*. Ekman (1914) discussed the difficulties inherent in the correct application of the name *V. arborescens*. The present treatment is in accord with Ekman's detailed history of the correct name for *V. arborescens*.

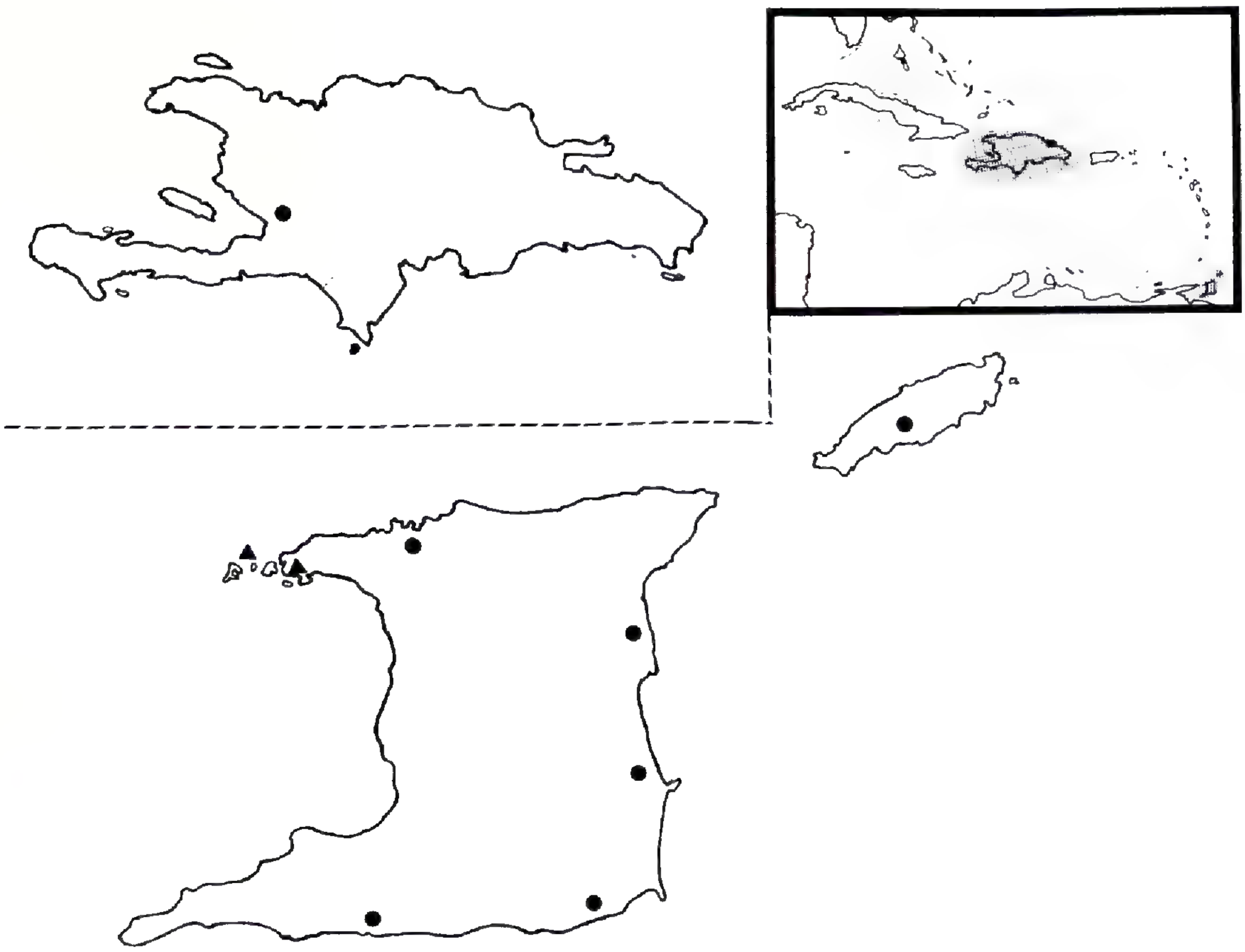
The type of *Vernonia arborescens β ovatifolia* does not represent a Cuban distribution for this species, but rather a description of a plant collected probably in Martinique and grown in the Botanical Garden in Havana. De la Ossa was the director of the Botanical Garden and presumably cultivated plants from various parts of the West Indies. Several species are included in the G-DC collection under this trinomial. Only the de la Ossa collection represents *V. arborescens*.

12. **Vernonia trinitatis** Ekman, Ark. Bot. 13: 39. 1914. TYPE: Trinidad, 1888, *Hart 2036* (holotype, S!; isotype, K!).

Shrub, 1–2 meters high; stems green, ribbed to terete, often with white to brown villous pubescence. Leaves large and not crowded along main stems; petioles 2–5(–10) mm. long, densely pubescent; blades 4.7–14.4 cm. long, 2.5–6.8 cm. wide, length/width ratio ca. 2, widest at or just below the middle, elliptic, shiny, pilose-hispid with distinct pubescence on veins above, hirsute to sericeous below, apex acuminate to aristate, base rounded to cuneate, the margins entire, repand, occasionally revolute, some remotely denticulate. Inflorescences of scorpioid cymes; heads (16- to) 19- to 25-flowered, sessile; involucres campanulate, 5–7 mm. high, 6–10 mm. wide, the phyllaries glandular-pubescent, becoming less so with age, loosely appressed, green to brown, some with dark tips, the inner phyllaries lanceolate to elliptic, 5–7 mm. long, 1–2 mm. wide, with tips acuminate to aristate, generally less than 1 mm. long, the outer phyllaries lanceolate to subulate (1.6–)2.5–4 mm. long, 0.5–0.8(–1.1) mm. wide; pappus white, occasionally appearing dirty, the inner bristles 4.5–6(–8) mm. long, the outer pappus of fimbriate scales, (0.8–)1–1.8 mm. long; corollas 5.5–7 mm. long, lavender to white, with occasional resin dots on tips of petals; anthers 2.5–3 mm. long. Achenes ca. 2 mm. long, sericeous, ribbed. Chromosome number $n = 51_{II}$. Flowering and fruiting from December to March.

DISTRIBUTION. Found only in northwestern Trinidad in and around Teteron Bay, on rocky cliffs in red soil near the sea, between 25 and 100 meters (MAP 5).

REPRESENTATIVE SPECIMENS. **Trinidad:** Teteron Bay, near Chaguaramas, on overgrown roadside banks along the closed section of Western Main Rd. to Scotland Bay, *Keeley & Keeley 1933–1948* (GA).



MAP 5. Distribution of *Vernonia trinitatis* (triangles) and *V. scorpioides* (circles) in Trinidad and Tobago, and Haiti.

This species is unusual in that it is the first polyploid *Vernonia* found in the West Indies, and is photosynthetic even in older stems. Ekman (1914) postulated that this was the ancestral species for the ARBORESCENTES. This seems unlikely since it is a polyploid and all of the other members of this subsection are diploid. *Vernonia trinitatis* exists in natural populations only with protection afforded it by its location within the military base at Teteron Bay. The coastal islands, which reportedly had this species at one time, are now cleared of nearly all vegetation. The species is preserved in the yards of some local people for use in preparing cough medicines and a syrup used in treating colds. The common name is "man better man."

13. **Vernonia orbicularis** Alain, Contr. Ocas. Mus. Colegio "De La Salle" **18**: 15, 16. 1960. TYPE: Cuba. Oriente Prov., Pinares, Mina Johnson, Moa, 20 July 1947, *Leon & Clemente 23210* (holotype, LS; isotype, NY!).

Vernonia leonis Alain, *ibid.* 14. TYPE: Cuba. Oriente Prov., sur de la region de Baracoa, 17 July–4 Aug. 1924, *Leon 12088* (holotype, LS; isotype, NY!).

Shrub, 0.7–1 meter high; stems densely pubescent. Leaves crowded near heads, cauline leaves evenly distributed; petioles 3–6 mm. long, densely pubescent; blades 1–3 cm. long, 1–2 cm. wide, length/width ratio ca. 1,

widest at or below the middle, broadly ovate to orbicular, dark green, shiny in some, sparsely pustulate-pubescent and with occasional long trichomes above, light yellow-green and densely villous to villous-hirsute below, apex obtuse to blunt, base rounded, the margins entire, sometimes revolute. Inflorescences of scorpioid cymes often greatly compacted; heads 9- to 12-flowered, sessile; involucres campanulate, 3–6 mm. high, 4–6 mm. wide, the phyllaries hirsute to villous, loosely appressed at maturity, gold to brown with occasional purple tips, the inner phyllaries lanceolate, 3.5–5.5 mm. long, 0.5–1 mm. wide, with tips acute, sometimes recurved, the outer phyllaries lanceolate, 0.5–2 mm. long, 0.5–0.8 mm. wide; pappus straw colored to clear white, the inner bristles 3–5 mm. long, the outer pappus of fimbriate scales, 0.9–1.6 mm. long; corollas 6–7.5 mm. long, purple to lavender, sparsely dotted with white trichomes; anthers 1.5–2.5 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed. Flowering and fruiting throughout the year.

DISTRIBUTION. Serpentine barrens and pinelands, from sea level to 900 meters, in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Région de Moa, sur la charrascal serpentineux de la Playa de la Vaca, *Victorin, Clemente, & Alain 21466* (NY, US); Guantánamo, Monte Libanon, San Fernández, *Ekman 10260* (F, NY).

This species is easily recognized by its orbicular leaves that are peculiarly yellow-green beneath, and by the dense tomentum on the stems and leaves. It is similar to *Vernonia leptoclada*, however, and may be a variant. The leaf shape and inflorescence of *Vernonia orbicularis* recalls the Jamaican Permolles form of *V. divaricata* which was first described as a distinct species (Gleason, 1906) until field work proved this distinction to be artificial. Observations of populations in the field would be very helpful here.

14. **Vernonia leptoclada** Schultz-Bipontinus, Jour. Bot. London 1: 233, 234. 1863. TYPE: Cuba. In Cuba orientali, 1860, *Wright 1309* (holotype, P; isotypes, GH!, GOET!, MO!).

Vernonia wrightii sensu Grisebach, Cat. Pl. Cubens. 144. 1866, non *V. wrightii* Schultz-Bipontinus, 1863.

Vernonia gnaphaliifolia sensu Gleason, Bull. N. Y. Bot. Gard. **4:** 178. 1906, p.p., non *V. gnaphaliifolia* Richard, 1850.

Vernonia calida Gleason, Bull. Torrey Bot. Club **40:** 318, 319. 1913. TYPE: Cuba. Oriente Prov., Sabanilla to Yamuri Arriba, 30 Jan.–1 Feb. 1911, *Shafer 8408* (holotype, NY!; isotypes, F!, GH!).

Vernonia calophylla Gleason, *ibid.* 317. TYPE: Cuba. Oriente Prov., Camp La Gloria, Sierra Moa, 24–30 Dec. 1910, *Shafer 8102* (holotype, NY!; isotype, US!).

Vernonia semitalis Gleason, *ibid.* 319. TYPE: Cuba. Oriente Prov., trail Río Yamaniguey to Camp Toa, 22–26 Feb. 1910, *Shafer 4176* (holotype, NY!).

Vernonia vicina Gleason, *ibid.* 317, 318. TYPE: Cuba. Oriente Prov., Camp

La Gloria, S. of Sierra Moa, 24–30 Dec. 1910, *Shafer 8202* (holotype, NY!).

Vernonia neglecta Gleason, *ibid.* 318. TYPE: Cuba. In Cuba Orientali, 1859–1860, *Wright 1309* (holotype, GH!).

Vernonia cristalensis Alain, Contr. Ocas. Mus. Colegio "De la Salle" **18:** 13, 14. 1960. TYPE: Cuba. Oriente Prov., Mayari on the crest of El Cristal, 2–7 April 1956, *Alain, Acuña, & Figueras 5609* (holotype, LS; isotype, NY!).

Vernonia acuñae Alain, *ibid.* 13–16. TYPE: Cuba. Oriente Prov., Pinares, Mina Johnson, 20 July 1947, *Leon & Clemente 23182* (isotype, NY!).

Vernonia moaensis Alain, *ibid.* 14. TYPE: Cuba. Oriente Prov., Pinelands, Moa, Jan. 1943, *Leon 21289* (holotype, LS; isotype, NY!).

Shrub, ca. 2 meters high; stems densely pubescent, yellow to brown. Leaves not crowded along main stems, subbracteal leaves similar to cauline but smaller, highly variable; petioles 1–2.5 cm. long, densely tomentose; blades 2–4 cm. long, 1.5–3.5 cm. wide, length/width ratio ca. 2, widest at or below the middle, ovate to elliptic, occasionally lanceolate, rugose to smooth, occasionally pustulate, with sparse white trichomes above, densely and closely glandular-pubescent, appearing grainy, with prominently pubescent veins below, the apex obtuse to acute, the base rounded to subcordate, rarely cuneate, the margins subcrenate to entire, often revolute. Inflorescence cymose, cymes variably scorpioid to relaxed divaricate; heads (11- to) 15- to 25-flowered, sessile; involucres campanulate, 5–8 mm. high, 6–8 mm. wide, the phyllaries often tomentose, loosely appressed at maturity, gold to brown, with prominent nerve and dark tips in some, the inner phyllaries linear to linear-lanceolate, 4–6.5 mm. long, 0.5–1.5 mm. wide, with tips acute, occasionally recurved; the outer phyllaries awl shaped to ovate, 1.5–2 mm. long, 0.5–0.8 mm. wide, with prominent central nerve; pappus white to dirty white, the inner bristles 3–5 mm. long, the outer pappus of fimbriate scales, 1–1.5 mm. long; corollas 5.5–9 mm. long, lavender to purple, occasionally gland dotted; anthers 1.5–2 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed. Flowering and fruiting throughout the year.

DISTRIBUTION. Serpentine barrens, pinelands, and areas of limestone soils, between 400 and 900 meters, in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Moa, plateau entre le Río Cananas et le Río Moa, *Victorin & Clemente 21744* (US); Baracoa, on the path to Florida, *Ekman 3504* (F, GH, NY, S).

There was apparently an interchange of Wright's numbers *284* and *1309* at the Cosson-Durand Herbarium in Paris. Grisebach misidentified *Vernonia leptoclada* as *V. Wrightii*. This error was further elaborated upon by Gleason (1906) in his treatment of *Vernonia gnaphaliifolia*. Ekman (1914; pages 16, 17) gave a more detailed account of the circumstances of this interchange.

This species, *Vernonia leptoclada*, constitutes one of the most variable assemblages of specimens yet encountered in the West Indies. It is found in an area of serpentine soils and appears to be part of a complex that includes *Vernonia desiliens*, *V. orbicularis*, and *V. pineticola*. These species

may all be endemic to this area, but they appear to hybridize to some degree as well and may represent only two rather polymorphic species. *Vernonia pineticola* is quite distinct, and its pollen is different from that of the others. *Ekman 3714*, *3715*, *3543*, and *6797* appear to represent various hybrids. *Vernonia yunquensis* occurs in this area, too, and may also be a hybrid; if this is so, the parental types are not clearly identifiable. *Vernonia leptoclada* and its allies in Oriente Province should definitely be reexamined in the field, since the treatment presented here is not definitive.

15. **Vernonia jenssenii** Ekman ex Urban, Repert. Sp. Nov. 26: 98, 99. 1929. TYPE: Cuba. Oriente Prov., in hills near Río Sagua, 7 Nov. 1916, *Ekman 8261* (holotype, S!; isotypes, BM!, F!, GH!, K!, MO!, NY!).

Shrub, ca. 1 meter high; stems ribbed, with dense tomentum. Leaves evenly spaced along main stems, sessile or with densely tomentose petioles to 2 cm. long; blades 2.8–4.8 cm. long, 1.4–1.6 cm. wide, length/width ratio ca. 2, widest at or slightly below the middle, lanceolate to ovate, hirsute, rugose and slightly bullate above, densely white-tomentose below, apex acute to acuminate, base rounded, margins entire. Inflorescences of loose, terminally branched scorpioid cymes; heads 21- to 25-flowered, sessile; involucres campanulate, 6–7 mm. high, 7–10 mm. wide, the phyllaries recurved, loosely appressed, pale yellow-green, the inner phyllaries ovate to ovate-lanceolate, 5.5–6 mm. long, 1–1.4 mm. wide, tips acute, the outer phyllaries awl shaped, recurved, 3.2–4.7 mm. long, 0.4–0.5 mm. wide, with tips 1–3 mm. long, sharply pointed; pappus pale yellow to white, the inner bristles 4–5 mm. long, the outer pappus of broad, fimbriate scales, 0.4–0.6 mm. long; corollas 6.3–6.5 mm. long, purple, glabrous; anthers 1.7 mm. long. Achenes 1–1.3 mm. long, sericeous, ribbed. Flowering and fruiting in November and December.

DISTRIBUTION. Pastures and steep hillsides, Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMEN. **Cuba.** ORIENTE PROV.: Sierra Maestra, Daiquiri, in pastures, *Ekman 8340* (NY).

Few specimens of this species were available for examination. It is very similar to *Vernonia leptoclada* except for the recurved phyllaries. It may, in fact, be but an odd variant of this latter species; for the moment it can be separated from *Vernonia leptoclada* in the herbarium and will therefore be maintained as a species; its status should, however, be reevaluated in light of field work when this is possible.

16. **Vernonia urbaniana** Ekman ex Urban, Repert. Sp. Nov. 26: 99. 1929. TYPE: Cuba. Oriente Prov., Sierra de Nipe, in thickets around Río Piloto, 10 Nov. 1919, *Ekman 10083* (holotype, S!; isotype, US!).

Shrub, ca. 1 meter tall; stems densely pubescent, becoming glabrate with age, ribbed. Leaves sparse along main stem, smaller and more numerous on terminal branches; petioles 2–3 mm. long, variously pubescent; blades 4.2–6.8 cm. long, 0.7–2 cm. wide, length/width ratio ca. 5, widest at or slightly below the middle, lanceolate to oblong-elliptic, rugose, glandular-punctate and shiny above, glabrous below except on veins, which are densely pubescent and resin dotted, apex acuminate, base cuneate to rounded, the margins entire, often revolute. Inflorescences of divaricate, scorpioid cymes; heads 15- to 20- (to 22-)flowered, sessile; involucres campanulate, 5–6 mm. high, 7–8.5 mm. wide, the phyllaries closely pubescent, firmly appressed, golden to brown, the inner phyllaries broadly oblong to rhomboid, fimbriate, 4.8–5.8 mm. long, 0.9–1.7 mm. wide, tips blunt to gradually acute, the outer phyllaries deltoid, 1–1.4 mm. long, 0.5–0.7 mm. wide; pappus white to straw colored, inner bristles 4–4.8 mm. long, outer bristles 0.6–1 mm. long; corollas 7–7.5 mm. long, lavender to purple, glabrous; anthers 1.8–2.5 mm. long. Achenes 1–3 mm. long, sericeous, ribbed. Flowering and fruiting throughout the year.

DISTRIBUTION. Steep hillsides and banks in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Sierra de Nipe, on a hillside at Río Piloto, *Ekman 5018* (F, S); Río Piloto, *Ekman 3338* (GH, NY, S, US).

There are few specimens of *Vernonia urbaniana* extant, and its distribution appears to be quite local. Since this species is sympatric with several other species in the ARBORESCENTES, it is possible that it is either a hybrid or a more variable series of collections that should be included under *Vernonia leptoclada*. This should be reexamined with field work in Cuba.

The name *Vernonia urbaniana* was reported to have been published in 1909 by Glaziou (Bull. Soc. Bot. France, Mém. 3). He did not treat Compositae in this publication, however, and nowhere mentioned *Vernonia*. Apparently the publication of this name was in error as was the proper date for the third mémoire in this series, which is 1905 rather than 1909. In the series in the University of Georgia, Athens, library, the third mémoire is bound in volumes 52 and 53, not 56 as previously cited.

17. **Vernonia desiliens** Gleason, Bull. Torrey Bot. Club 40: 316. 1913.
TYPE: Cuba. Oriente Prov., among rocks near water, Arroyo del Medio, above the falls, 20 Jan. 1910, *Shafer 3232* (holotype, NY!; isotypes, F!, GH!, MO!, S!, US!).

Shrub, 0.5–1.5 meters high; stems closely tomentose, sparsely so in places. Leaves decreasing in size near terminal heads, not crowded along main stem; petioles 2–5 mm. long, closely and sparsely tomentose; blades 2–8 cm. long, 1.5–3.5 cm. wide, length/width ratio ca. 3, but variable, widest below the middle, elliptic to lanceolate, dark green, sparsely pubescent above, light yellow-green and tomentose below, apex acute to oc-

casionally blunt, base rounded to cuneate, the margins entire to minutely crenate, revolute in some. Inflorescences of broad scorpioid cymes, sometimes sharply angled at point of flower head attachment; heads 20- to 30-(to 35-)flowered, sessile; involucres campanulate, 9–11 mm. high, (8–)9–11 mm. wide, the phyllaries sparsely pubescent to villous, resinous, loosely imbricated at maturity, dark gold-brown, often with darker tips, the inner phyllaries linear to ligulate, 7–9 mm. long, 1–1.5 mm. wide, with tips obtuse to acute, often recurved, the outer phyllaries deltoid, 1.5–2 mm. long, 0.6–1.2 mm. wide; pappus white, the inner bristles 5–6.5 mm. long, the outer pappus of fimbriate scales, 1–1.5 mm. long; corollas 7.5–8.5 mm. long, purple to lavender, glabrous; anthers 2.5 mm. long. Achenes 1.5–3 mm. long, sericeous, ribbed. Flowering and fruiting throughout the year.

DISTRIBUTION. Serpentine and limestone soils, pine barrens, and rocky areas, from 400 to 1200 meters, Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV. Sierra de Nipe: Loma Mensura, *Ekman 3178* (F, NY, S); headwaters of Brazo Dolores, *Ekman 3121* (GH, MO, US).

This species, *Vernonia desiliens*, is one of a group that occurs on serpentine soils in the mountains of Oriente Province. It has thick and rigid stems in comparison with the other species, and heads that appear heavy. It may hybridize with *Vernonia orbicularis*, *V. leptoclada*, and/or *V. pineticola*; field studies would be helpful in understanding the appearance of individuals with intermediate characteristics.

18. **Vernonia pineticola** Gleason, Bull. N. Y. Bot. Gard. 4: 176. 1906.
TYPE: Cuba. Oriente Prov., Baracoa, in pine woods, in clumps, March 1903, *Underwood & Earle 1341* (holotype, NY!).

Shrub, 1–2 meters high; stems densely pubescent, decreasing with age, ribbed, yellow-green. Leaves evenly spaced along main stems, more crowded on terminal branches; petioles 1–2 mm. long, densely pubescent; blades 1.5–4 cm. long, 1–2.5 cm. wide, length/width ratio ca. 1.5, widest below the middle, ovate to elliptic, rugose, pustulate with sparse pubescence, shiny above, woolly-tomentose and light yellow-green below, apex obtuse to blunt, base cuneate to subcordate, the margins entire, often revolute. Inflorescences of scorpioid cymes, often greatly extended; heads 15- to 20-flowered, sessile; involucres campanulate, 11–12.5 mm. high, 10–13 mm. wide, the phyllaries stiff, glabrous to woolly-pubescent, loosely appressed at maturity, rose-purple, the inner phyllaries awl shaped, 9.5–12.0 mm. long, 1–1.5 mm. wide, with tips acute, much tapered, the outer phyllaries awl shaped, 2.5–5 mm. long; pappus brown, the inner bristles 5–7 mm. long, 0.5–1 mm. wide, the outer pappus of fimbriate scales, 0.5–1 mm. long; corollas 7.5–10 mm. long, rose-purple, occasionally resin dotted; anthers 2.5–3 mm. long. Achenes 1.5–3 mm. long, sericeous, ribbed. Flowering and fruiting from March to December.

DISTRIBUTION. Pine barrens, serpentine and limestone soils, between 600 and 700 meters, in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Baracoa, pineland hill N. of El Yunque, *Ekman 3542* (F, MO, NY, S, TEX); Guantánamo, Monte Libanon, San Fernández, *Ekman 10268* (NY, S).

The distinctive spikelike phyllaries and their bright purple coloration set this species off from other sympatric taxa. *Vernonia pineticola* appears to hybridize with *Vernonia leptoclada* and its allies, however. Field observations would be helpful in clarifying the relationships of *V. pineticola* and others found in nearby areas. *Vernonia pineticola* has unusual spineless pollen grains and represents an offshoot from the main line of ARBORESCENTES (Keeley & Jones, 1977a).

19. **Vernonia yunquensis** Gleason, Bull. N. Y. Bot. Gard. 4: 191. 1906. TYPE: Cuba. Oriente Prov., El Yunque, Mt. Baracoa, March 1903, *Underwood & Earle 661* (holotype, NY!; isotype, GH!).

Shrub, 1–2 meters tall; stems densely tomentose to villous, light yellow-green. Leaves crowded near terminal heads, less so along main stem; petioles 0.2–0.5 mm. long, densely pubescent; blades 3.5–5 cm. long, 2–2.5 cm. wide, length/width ratio ca. 2, widest at or slightly below the middle, elliptic to ovate, dark green, pustulate, shiny, sparsely pubescent above, light yellow-green, tomentose to villous below, apex acute to obtuse, base rounded to cuneate, margins entire. Inflorescences of divaricate scorpioid cymes, often much condensed; heads ca. 25-flowered, sessile; involucres campanulate, 8–10 mm. high, 6–8 mm. wide, the phyllaries white-tomentose to villous, loosely appressed, brown to purple with darker tips, the inner phyllaries rhomboid to linear-lanceolate, 6–7 mm. long, 1.5–2 mm. wide, with tips cuspidate to acute, recurved, the outer phyllaries lanceolate to elliptic, 1–1.5 mm. long, 0.5–0.8 mm. wide; pappus straw colored to white, the inner bristles ca. 4 mm. long, the outer pappus of fimbriate scales, 1.5 mm. long; corollas ca. 9 mm. long, rose-purple, gland dotted, with few sparse hairs; anthers 2–2.5 mm. long. Achenes ca. 3 mm. long, sericeous, ribbed. Flowering and fruiting from December to March.

DISTRIBUTION. El Yunque, Mt. Baracoa, near top of peak, Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMEN. **Cuba.** ORIENTE PROV.: Baracoa, top of El Yunque, *Ekman 3962* (F, GH, NY).

Because of its greatly condensed inflorescences that form a clustered group of nearly sessile heads at the tops of the branches, this species appears distinct from others occurring in the area of Oriente Province. In addition, the heads are longer and the phyllaries more densely imbricate than in other species. There are very few collections of *Vernonia yun-*

quensis, which may actually represent a hybrid. This should be investigated when field work is possible.

20. **Vernonia gnaphaliifolia** Richard in Sagra, Hist. Fis. Pol. Nat. Cuba 2: 33, 34. 1850. TYPE: Cuba. Crescit prope Canasi, mense julio florens, *Sagra s.n.* (holotype, P!; isotype, F!).

Vernonia arborescens (Linnaeus) Swartz var. *divaricata* Grisebach, Cat. Pl. Cubens. 144. 1866. TYPE: Cuba. Pine woods, Los Remates, La Cipa, Dec. 1860–64, *Wright 2787* (holotype, GOET!; isotypes, GH!, MO!).

Vernonia membranacea Grisebach, *ibid.* 144, 145. TYPE: Cuba Occ. [Cuba], 1863, *Wright s.n.* (#490 was apparently added later to this label) (holotype, GOET!; isotype, GH!).

Vernonia crassinervia Wright ex Gleason, Bull. N. Y. Bot. Gard. **4:** 180. 1906. TYPE: Cuba. Pine woods, Los Remates, La Cipa, Dec. 1860–64, *Wright 2787* (holotype, GOET!; isotypes, GH!, MO!).

Vernonia sublanata Gleason, *ibid.* 177. TYPE: Cuba. Vicinity of Madruga, 28 March 1903, *Britton, Britton, & Shafer 784* (holotype, NY!).

Vernonia sublanata var. *angustata* Gleason, *ibid.* 177, 178. 1906. TYPE: Cuba. Oriente Prov., dry hill, Santiago, March 1903, *Underwood & Earle 202* (holotype, NY!).

Vernonia angustata Gleason, Bull. Torrey Bot. Club **40:** 309. 1913.

Vernonia gnaphaliifolia Richard var. *platyphylla* Gleason, *ibid.* **46:** 238. 1919. TYPE: Cuba. Oriente Prov., Enseñada de Mora, 26–29 March 1912, *Britton, Cowell, & Shafer 12933* (holotype, NY!).

Vernonia platyphylla (Gleason) Ekman ex Urban, Repert. Sp. Nov. **26:** 100. 1929.

Vernonia nervosa Alain, Contr. Ocas. Mus. Colegio "De la Salle" **18:** 150. 1960. TYPE: Cuba. Oriente Prov., "El Cerrito," an eruptive hill between Zarzal and Nagua, 12 April 1915, *Ekman 5378* (holotype, LS; isotypes, GH!, NY!, US!).

Shrub, 1–2 meters high; stems thinly pubescent to tomentose on youngest branches. Leaves sparse along main stems, more numerous on terminal branches; petioles 1–4 mm. long, pubescent; blades 2.9–9.2 cm. long, 0.8–2 cm. wide, length/width ratio ca. 3, widest at or just below the middle, oblong, ovate to linear-lanceolate, dark green, glandular-punctate, sparsely tomentose and rugose above, closely sericeous to tomentose below, veins prominent, apex acute to obtuse, base tapering to cuneate, the margins undulate or repand, often revolute. Inflorescences of branched cymes; heads 16- to 25- (to 33-)flowered, sessile or with peduncles to 2 mm. long; involucres campanulate, 6–7 mm. high, 7–12 mm. wide, the phyllaries hirsute to villous, resin dotted, loosely appressed, reflexed at maturity, golden to golden-brown, the inner phyllaries ovate to lanceolate, rarely rhomboid, 5–6.9 mm. long, 0.8–1.3 mm. wide, tips acuminate, the outer phyllaries awl shaped to subulate, 1.3–3.2 mm. long, 0.3–0.6 mm. wide; pappus white to slightly dirty white, inner bristles 4–6 mm. long, outer bristles 0.5–1 mm. long; corollas 6–7.5 mm. long, lavender to purple, resin dotted at tips of petals; anthers 1.5–2 mm. long. Achenes ca. 3 mm.

long, with numerous short, stiff hairs, resinous, ribbed. Flowering and fruiting throughout the year.

DISTRIBUTION. Serpentine soils, near roadsides in the mountains, between 300 and 600 meters, in Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** CAMAGÜEY PROV.: Sierra Cubitas to Santa Rosa, *Shafer 541* (NY). LA HABANA PROV.: Tetas de Camarioca, Matanzas, *Britton, Britton, & Wilson 14004* (F, GH, MO, NY, US). ORIENTE PROV.: Holguín, Cerro de Fraile, *Ekman 3224* (F, GH, MO, NY, S, US). PINAR DEL RÍO PROV.: Bahía Honda, S. of town, *Ekman 10421* (F, GH, NY, US). SANTA CLARA PROV.: Pozo de la Bermuda, W. of Manacas, *Leon & Cazanas 5847* (NY). ISLA DE PINOS: Lomas de Cañada, *Ekman 12133* (NY).

This is a highly variable species found throughout Cuba. The numerous taxa that have been described previously and placed into synonymy with *Vernonia gnaphaliifolia* attest to its variability. Field collections would greatly improve our understanding of this polymorphic species.

21. **Vernonia fruticosa** (Linnaeus) Swartz, Fl. Ind. Occ. 3: 1323. 1806.

Conyza fruticosa Linnaeus, Sp. Pl. ed. 2. 1209. 1763. TYPE: based on C. Plumier (ed. J. Burmann), Pl. Amer. 83, 84. *t. 95, fig. 1.* 1756.
Cacalia fruticosa (Linnaeus) Kuntze, Rev. Gen. Pl. **2:** 968. 1891.
Vernonia buchii Urban, Repert. Sp. Nov. **16:** 146. 1919. TYPE: Haiti. Plaine Cul de Sac, March 1918, *Buch 1506* (isotype, GH!).

Shrub, 0.4–1.2 meters high; stems densely tomentose to hirsute, ribbed, resinous, light gray to brown. Leaves evenly distributed along main stems, often sparse; petioles 0.1–0.5 mm. long, gray to brown, tomentose; blades 0.8–2.5 cm. long, 0.4–1.8 cm. wide, length/width ratio ca. 2, widest below the middle, ovate to parabolic, rugose, covered with pustulate pubescence, often velvety above, velvety tomentose and with few glands below, the apex blunt, obtuse to retuse, the base rounded to subcordate, the margins entire to crenate or undulate, sometimes revolute. Inflorescences of extended cymes; heads 14- to 25-flowered, sessile or with densely tomentose to hirsute peduncles to 2 mm. long; involucres campanulate, 4.5–7 mm. high, 4–7 mm. wide, the phyllaries pubescent, spreading to reflexed at maturity, golden brown, the inner phyllaries lanceolate to rhomboid, 4.5–6.5 mm. long, 1–1.5 mm. wide, with tips acute, often recurved, the outer phyllaries awl to needle shaped, 0.8–2.9 mm. long, 0.1–0.5 mm. wide; pappus white, the inner bristles 3.5–5 mm. long, the outer pappus of fimbriate scales, 0.3–1 mm. long; corollas 5–7 mm. long, white to lavender, glabrous; anthers ca. 2 mm. long. Achenes ca. 3 mm. long, sericeous ribbed. Chromosome number $n = 17$. Flowering and fruiting throughout the year.

DISTRIBUTION. Pinelands or open hillsides, on limestone, bauxite, and serpentine soils, between 1200 and 1300 meters, in the mountains of Haiti and the Dominican Republic (MAP 4).

REPRESENTATIVE SPECIMENS. **Dominican Republic.** AZUA PROV.: Sierra de Ocoa, San José de Ocoa, Bejucal, *Ekman 12047* (F, GH, NY, S). BARAHONA PROV.: *Fuertes 655* (F, GH, MO, NY, S, US). LA VEGA PROV.: serpentine barrens, Barrancón, from Banao to Hato Viejo, *Liogier 14838* (NY). MONTE CRISTI PROV.: Cordillera Central Monción, *Ekman 13011* (S, US, TEX). PEDERNALES PROV.: near El Pon on the way to Aceitillar, Sierra del Bahoruco near Pedernales, *Liogier 13791* (GH, NY). SANTIAGO PROV.: Guatara de Chino, Monte Jicomé, *Valeur 298* (S). **Haiti.** DÉPART DU NORD-OUEST: presqu'île du Nord-Ouest, montagnes de Terre Nueve, top of Morne La Fortune, *Ekman 4979* (S, US). DÉPART DU SUD-OUEST: Port-au-Prince, *Ekman 3039* (S).

Vernonia fruticosa has a characteristic appearance and can be easily recognized by its sprawling habit and extremely rugose leaves. It is locally abundant, but otherwise rare in the highest mountains of Hispaniola. Some sheets of *Vernonia gnaphaliifolia*, a Cuban species, bear a strong resemblance to *V. fruticosa*, and relationships between these two taxa should be investigated when living material is obtainable.

22. **Vernonia complicata** Wright ex Grisebach, Cat. Pl. Cubens. 143. 1866. TYPE: Cuba, 1860–64, *Wright 2790* (holotype, K!; isotypes, GH!, MO!, NY!, S!).

Shrub, 5–10 dm. high; stems closely tomentose. Leaves crowded, especially on terminal branches; petioles 0.2–0.5 mm. long, closely tomentose; blades 0.5–1.5 cm. long, 0.6–1.5 cm. wide, length/width ratio ca. 1, widest at or above the middle, obovate, spatulate, or obcordate, softly tomentose and yellow-green above, softly tomentose and glandular, white to yellow-green below, the apex obtuse, emarginate to blunt, the base tapering to cuneate, the margins entire, typically very repand. Inflorescences terminal, usually solitary, rarely with two heads, in a divaricate cyme; heads 8- to 12-flowered, sessile; involucres campanulate, 4–5 mm. high, 4–5 mm. wide, the phyllaries softly tomentose to villous, firmly appressed until maturity, golden brown, the inner phyllaries awl shaped, tapering, (3–) 3.5–4.5 mm. long, 1–1.1 mm. wide, tips acute, the outer phyllaries broadly deltoid to awl shaped, pubescent, 1–2 mm. long, 0.3–0.5 mm. wide; pappus white to straw colored, the inner bristles (4–)5–6 mm. long, the outer pappus of fimbriate scales, 0.5–1 mm. long; corollas 6–9.6 mm. long, lavender to purple, glabrous; anthers 2–2.5 mm. long. Achenes 1.5–3 mm. long, ribbed, softly sericeous, hairs shiny. Flowering and fruiting from November to March.

DISTRIBUTION. Cliffs facing the ocean, in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Guantánamo, Caimanera W. of Emerald Pt. in wild cliffs facing the sea, *Ekman 15765* (F, GH, MO, NY); coastal cliffs, Leeward Pt., *Britton 2225* (GH, US).

This species appears to be most closely related to *Vernonia arbuscula* of the Bahamas. *Vernonia complicata* can easily be recognized and dis-

tinguished from all other Caribbean vernonias by its low growth habit and its conspicuously repand leaves.

23. **Vernonia arbuscula** Lessing, Linnaea 6: 664. 1831.

Synonymies, typifications, and representative specimens are given in Keeley and Jones (1977b).

Shrub up to 3 meters tall; stems gray- to brown-tomentose, gland dotted, often much branched at least terminally. Leaves crowded, especially on terminal branches; petioles 6–8 mm. long, gray-brown-tomentose and glandular; blades 1.5–2(–4) cm. long, 0.6–1.5(–2.2) cm. wide, length/width ratio ca. 1.5, widest above the middle, spatulate, obovate, obcordate, to lanceolate, surface gray-green-tomentose, gland dotted, upper surface frequently darker and greener in appearance than lower surface, which occasionally appears whitish, the apex acute to blunt, retuse, emarginate to obcordate, the base tapering, the margins entire to repand. Inflorescences much condensed on terminal cymes, usually with 3 to 5 heads; heads 8- to 12-flowered, sessile; involucres campanulate, 4–5 mm. high, 4–5 mm. wide, the phyllaries tomentose to villous, closely appressed when immature, golden brown, the inner phyllaries awl shaped, 3.5–4 mm. long, 1–1.5 mm. wide, tomentose to villous, with conspicuous resinous dots, with tips tapering, acute, the outer phyllaries broadly awl shaped, densely pubescent, size variable with age; pappus whitish to straw colored, the inner bristles 5–6 mm. long, the outer pappus of fimbriate scales, 0.5–1 mm. long, with jagged, often deeply cleft edges; corollas 6–9 mm. long, violet to rose-purple, with a smooth surface; anthers (1.5–)2.5–3.2 mm. long. Achenes 2–3.5 mm. long, with 5 to 10 ribs (5 larger or 10 smaller), sericeous to hirsute, hairs shiny. Chromosome number $n = 17$. Flowering and fruiting throughout the year.

DISTRIBUTION. Limestone areas in pinewoods and clearings throughout the Bahamas.

This species is highly variable, especially with regard to leaf shape. A full treatment of the differences is given in Keeley and Jones (1977b).

24. **Vernonia stenophylla** Lessing, Linnaea 6: 667, 668. 1831. TYPE: Dominican Republic. Barahona Prov., prope Las Salinas ad ripam fluminis, Oct. 1911, *Fuertes 1392* (isoneotypes (here designated), F!, GH!, MO!, NY!, S!, US!).

Vernonia remotiflora forma *angustifolia* Grisebach, Cat. Pl. Cubens. 144. 1866, p.p. TYPE: Cuba, 1860, *Wright 2786* (holotype, GOET!; isotype, TEX!).
Cacalia stenophylla (Lessing) Kuntze, Rev. Gen. Pl. 2: 971. 1891.
Vernonia corallophila Gleason, Bull. Torrey Bot. Club **40:** 309. 1913. TYPE: Cuba. Oriente Prov., U. S. Naval Station, Guantanamo Bay, coral limestone cliffs, 17–30 March 1901, *Britton 1939* (holotype, NY!; isotypes, GH!, MO!, US!).
Vernonia nematophylla Ekman & Urban, Repert. Sp. Nov. **26:** 100, 101. 1929.

TYPE: Cuba. Oriente Prov., Sierra Maestra, near Alto Gracia, on the trail to Bacano, 4 Nov. 1916, *Ekman 8189* (holotype, S!; isotype, F!, NY!).

Shrub, ca. 1 meter high; stems strigose to sericeous, white to gray, becoming glabrate with age, barely ribbed to terete. Leaves evenly spaced, sometimes crowded at a node in a fascicular arrangement; petioles less than 1 mm. long, pubescent; blades 3–10 cm. long, 0.1–0.8 cm. wide, length/width ratio ca. 30, widest slightly below the middle, linear-lanceolate, shiny, with strigose hairs with persistent pustulate bases, hirsute above with main vein sunken, white sericeous below, the apex acute to mucronate, with main vein extending into point, the base cuneate to tapering, with vein widest at the base, frequently making up much of the basal width, the margins conspicuously revolute. Inflorescences racemose, heads on much-reduced cymes; heads (11- to) 17- to 22-flowered, sessile; involucres campanulate, 5–6 mm. high, 7–8 mm. wide, the phyllaries sericeous, loosely appressed, pale green to gold at maturity, both series of equal length, the inner phyllaries lanceolate to elliptic, 4.7–5.3 mm. long, 0.6–1 mm. wide, tips narrowly acute, the outer phyllaries lanceolate to linear-lanceolate, 2–4 mm. long, 0.4–0.6 mm. wide; pappus brown, inner bristles 4–5 mm. long, outer bristles 0.5–0.7 mm. long; corollas 5.5–6 mm. long, lavender to white, glabrous; anthers ca. 1.5 mm. long. Achenes ca. 2 mm. long, sericeous, occasionally glandular, obscurely ribbed. Flowering and fruiting throughout the year, but chiefly between September and December.

DISTRIBUTION. Dry limestone hills and banks, from 25 to 900 meters, in Cuba and central Hispaniola (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: U.S. Naval Station, Guantanamo Bay, *Britton 1939* (F, GH, MO, NY, US). **Dominican Republic.** BAHORUCO PROV.: El Cercado, serpentine barrens S. of town, *Liogier 12476* (GH, NY, US). LA VEGA PROV.: Cordillera Central, La Vega W. of Río Yaque, *Ekman 14162* (S, TEX). MONTE CRISTI PROV.: El Morro, *Liogier 15630* (NY, US). SANTIAGO PROV.: Pinar de Caimito, ca. 5 mi. NW. of San José de las Matas, *Liogier 16277* (GH, NY). **Haiti.** DÉPART DE L'ARTIBONITE: vicinity of Ennery, *Leonard 9011* (NY, US). DÉPART DU NORD: vicinity of St. Michel de l'Atalaye, *Leonard 7168* (GH, NY). DÉPART DU NORD-OUEST: vicinity of Jean Rabel, *Leonard & Leonard 12926* (MO, US). DÉPART DU SUD-OUEST: Port-au-Prince, Monfleurs, *Ekman 1993* (F, GH, NY, S).

The loosely imbricate, subequal phyllaries distinguish *Vernonia stenophylla* from other narrow-leaved taxa in Cuba and the Dominican Republic. It is predominantly in Hispaniola and was previously found in Cuba at Guantanamo Bay, where it may now be extinct.

25. **Vernonia commutata** Ekman, Ark. Bot. 13: 77, 78. 1914. TYPE: Cuba. In Cuba Orientali, 1856–57, *Wright 286* (holotype, K!; isotypes, F!, GH!, M!, NY!).

Vernonia araripensis sensu Gleason, Bull. N. Y. Bot. Gard. 4: 181. 1906, non *V. araripensis* Gardner, 1846.

Vernonia remotiflora forma *angustifolia* Grisebach, Cat. Pl. Cubens. 144. 1866, p.p., non *V. remotiflora* Richard, 1792. TYPE: Cuba. In Cuba Orientali, 1856–57, *Wright 286* (holotype, K!).

Shrub, 1–1.5 meters tall; stems ribbed, often with appressed gray pubescence. Leaves uncrowded at least along the main stem, subbracteate leaves similar to but smaller than the cauline; petioles 1–3 mm. long, finely strigose- or hispid-pubescent; blades 1–8 cm. long, 0.2–0.8 cm. wide, length/width ratio ca. 2, widest at or slightly below the middle, linear to linear-lanceolate, shiny, pustulate-pubescent to glabrate in older leaves, rugose and dark green above, glandular and resinous with pronounced pubescent veins below, apex acute to obtuse, base cuneate to tapering, the margins revolute, repand, entire. Inflorescences of scorpioid cymes; heads 17- to 21-flowered, sessile or with peduncles to 1 mm. long; involucres campanulate, 4–5 mm. high, 5–7 mm. wide, the phyllaries finely pubescent, becoming glabrate with age, loosely appressed, golden to light brown, often with purple tips, the inner phyllaries lanceolate to elliptic, 3.8–5 mm. long, 0.8–1 mm. wide, with tips acute to acuminate, often continued from central nerve, the outer phyllaries deltoid to lanceolate, 1–1.5 mm. long, 0.3–0.5 mm. wide; pappus white, the inner bristles ca. 4 mm. long, the outer pappus of fimbriate scales, 0.5–0.7 mm. long; corollas 5.5–6 mm. long, lavender to purple, glabrous; anthers 1.2–1.5 mm. long. Achenes ca. 2 mm. long, sericeous, faintly ribbed. Flowering and fruiting from November to March.

DISTRIBUTION. Open pinelands and forests, from 400 to 800 meters, in Oriente Province, Cuba (MAP 4).

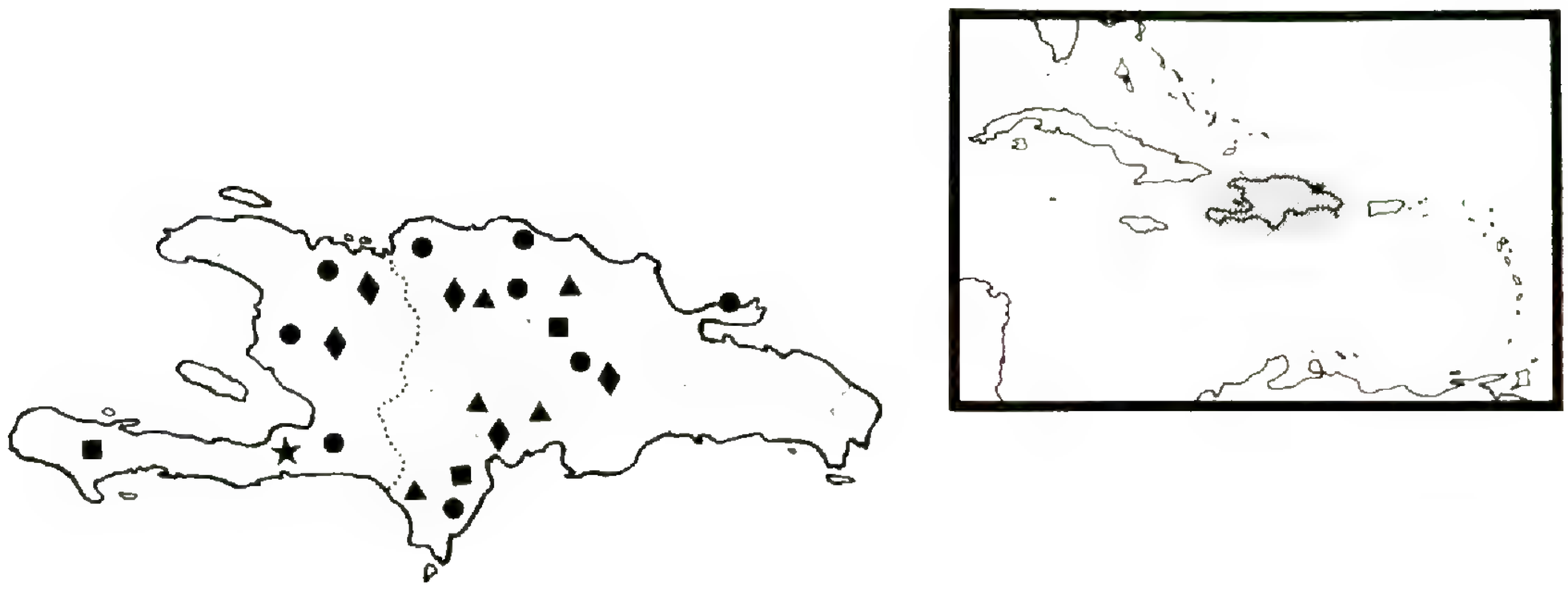
REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: Bayamo, Corojo, El Pinar, *Ekman 5066* (GH, MO, NY, S); pinelands vicinity of El Cuero, *Britton & Cowell 12758* (F, NY, US).

Vernonia commutata is very similar to *Vernonia sericea* and *V. stenophylla* and almost appears to be a glabrate variety of *V. sericea*. It can, however, be separated from this species by the lack of leaf pubescence.

Subsection II. BUXIFOLIAE

26. **Vernonia barkeri** Ekman ex Urban, Ark. Bot. **23A**: 49. 1931. TYPE: Haiti. Plaine Cul-de-Sac, Ganthier, riverbed of Rivière Blanche, 12 Dec. 1926, *Ekman 7351* (holotype, S!; isotypes, F!, GH!, NY!, S!, US!).

Shrub, 1–4 meters high; stems densely and closely pubescent, becoming glabrate with age, gray to brown, ribbed. Leaves not crowded along main stems, most leaves on terminal branches; petioles 1–5 mm. long, with lanate to glandular tomentum; blades 1.4–3 cm. long, 0.9–1.6 cm. wide, length/width ratio ca. 1.5, widest at or above the middle, broadly spatulate, shining, with numerous sunken glands above, pilose to hispid, with many resinous glands below, apex rounded to acute, base



MAP 6. Distribution of *Vernonia barkeri* (squares), *V. buxifolia* (circles), *V. tuerckheimii* (triangles), *V. ekmanii* (star), and *V. sprengeliana* (diamonds) in Haiti and the Dominican Republic.

tapering, margins entire. Inflorescences in terminal cymes, often with clusters of 3 to 5 heads; heads 10- to 14-flowered, the peduncles 3–10 mm. long, covered with dense, glandular pubescence; involucres campanulate to turbinate, 3–5 mm. high, 4–6 mm. wide, the phyllaries variously pubescent, with long hairs prominent along margins, some glandular and sticky, tightly appressed, green to brown, the inner phyllaries linear to linear-lanceolate, 3–4.1 mm. long, 0.8–1.2 mm. wide, with tips usually acuminate, but occasionally cuspidate; the outer phyllaries deltoid, 0.5–0.8 mm. long, 0.4–0.6 mm. wide; pappus yellow to white, inner bristles (4–)5–6 mm. long; corollas 6–7 mm. long, white to lavender, with resinous dots on petal tips; anthers 3–4 mm. long. Achenes 1.8–2.5 mm. long, glabrous, with resinous glands, ribbed. Flowering and fruiting throughout the year.

DISTRIBUTION. Dry, rocky soils, 100 to 250 meters, in Haiti and the Dominican Republic (MAP 6).

REPRESENTATIVE SPECIMENS. **Dominican Republic.** BARAHONA PROV.: prope Las Salinas et Ferrusco, *Fuertes 1394* (US). LA VEGA PROV.: in thickets, El Número, near Azua, *Liogier 16604* (GH, NY, US). **Haiti.** DÉPART DU SUD-OUEST: vicinity of Fond Parisien, Étang Saumâtre, *Leonard 10142* (GH, US).

Vernonia barkeri can easily be recognized by the lack of a distinct outer series of pappus bristles, as well as by some vegetative features. It is one of the few West Indian vernonias growing in an arid environment.

27. **Vernonia buxifolia** (Cassini) Lessing, Linnaea **4**: 313. 1829.

Lepidaploa buxifolia Cassini, Dict. Sci. Nat. **26:** 18, 19. 1823. TYPE: Dominican Republic, *Desfontaines s.n.* (holotype, FI).
Vernonia domingensis de Candolle, Prodr. **5:** 30. 1836. TYPE: Dominican Republic, 1821, *Balbis s.n.* (holotype, G-DC (IDC B–800–2. 767: I. 4!)).
Eupatorium domingense Sprengel ex de Candolle, *ibid.*
Proustia domingensis Sprengel ex de Candolle, *ibid.*
Cacalia buxifolia (Cassini) Kuntze, Rev. Gen. Pl. **2:** 969. 1891.

Vernonia montana Gleason, Bull. N. Y. Bot. Gard. **4:** 191. 1906. TYPE: Haiti. Le Brande to Mt. Balance, 15 Aug. 1905, *Nash & Taylor 1756* (holotype, NY!).

Shrub, 2–5 meters high; stems finely gray- or brown-pubescent, resin dotted. Leaves crowded in young shoots, often at terminal ends of branches; sessile or with resin-dotted, finely pubescent petioles to 0.5 mm. long; blades 0.5–2.5 cm. long, 0.5–1.8 cm. wide, length/width ratio ca. 1.5, widest at or above the middle, rarely wider below, broadly ovate to rhomboid to elliptic, shiny, glandular-punctate, occasionally with sparse pubescence above, finely tomentose, occasionally resinous, punctate below, the apex acute to mucronate, the base constricted, cuneate, the margins entire or with 3 to 5 small teeth. Inflorescences subumbellate; heads 5- to 14-flowered, the peduncles 2–4 mm. long, resinous, sparsely pubescent; involucres turbinate, 3–10 mm. high, 5–8 mm. wide; the phyllaries finely pubescent, resin dotted, loosely appressed at top, persistent at base, golden to brown, the inner phyllaries linear to narrowly awl shaped, 2–7 mm. long, 0.6–1.3 mm. wide, tips acute, the outer phyllaries orbicular to roundly deltoid, 0.6–1.5 mm. long, 0.4–1.2 mm. wide; pappus yellow to orange, inner bristles 4–7 mm. long, outer bristles 0.5–0.7 mm. long; corollas 8–11 mm. long, white to purple, glabrous; anthers ca. 3 mm. long. Achenes ca. 4 mm. long, ribbed, resin dotted. Flowering and fruiting throughout the year.

DISTRIBUTION. Limestone soils in wet areas of mountain forests and pine barrens, from 150 to 900 meters, throughout the Cordillera Central of Hispaniola (MAP 6).

REPRESENTATIVE SPECIMENS. **Dominican Republic.** BARAHONA PROV.: La Hotte, between La Cueva and Placer Bonita, *Howard 12257* (GH, US). LA VEGA PROV.: El Montazo, from Constanza to Valle Nuevo, *Liogier 15432* (GH, NY, US). MONTE CRISTI PROV.: Moncíon, *Mera, Herb. Jiménez 1898* (US). PUERTA PLATA PROV.: Sierra de Yaroa, *Liogier 13559* (GH). SAMANA PROV.: vicinity of Laguna, Samana Peninsula on the Pilar de Azucar, *Abbott 2388* (NY, US). **Haiti.** DÉPART DE L'ARTIBONITE: Massif de Cahors, Petite Rivière de l'Artibonite, Rd. to Medor at Sferlin, *Ekman 3391* (S, US). DÉPART DU NORD: Bayeux Morne Brigand, in naked limestone rocks, *Ekman 2659* (S); vicinity of Dondon, *Leonard 8594* (F, MO). DÉPART DU SUD: Morne de la Hotte, in decliv. austral. Mont Ma Blanche, prope Dauyette, *Ekman 466* (GH, S, US).

The large, turbinate heads and orange pappus of *Vernonia buxifolia* distinguish it from the closely related *V. tuerckheimii*. Both species were apparently common in the past, but lumbering and slash and burn agricultural practices have reduced their ranges; *Vernonia buxifolia* is now restricted to high-elevation areas not accessible by road.

28. **Vernonia tuerckheimii** Urban, Symb. Antill. 7: 421, 422. 1912. TYPE: Dominican Republic. La Vega Prov., prope Constanza, 1250 m. in declivibus pineti, Feb. 1910, *Tuerckheim 2959* (holotype, S; isotype, NY!).

Vernonia microphylla Alain, Mem. N. Y. Bot. Gard. **21**: 156. 1971. TYPE: Dominican Republic. Bahoruco Prov., El Cercado, serpentine barrens on hillside S. of town, 4 Sept. 1968, *Liogier 12477* (holotype, NY!; isotypes, GH!, US!).

Vernonia pusilliflora Alain, Phytologia **25**: 279. 1973. TYPE: Dominican Republic. Pedernales Prov., Aceitillar, Cayo, Bahoruco Mts., 26 Feb. 1971, *Liogier 17916* (holotype, NY!).

Shrub, 1–2 meters high; stems ribbed, gray to brown, finely tomentose, occasionally resinous. Leaves sparse on main stems, crowded on lateral branches and below inflorescences; petioles 1–2 mm. long, densely white-tomentose; blades 0.5–1.2 cm. long, 0.5–0.9 cm. wide, length/width ratio ca. 1.2, widest at or above the middle, obovate to broadly elliptic, shiny and glandular-punctate above, densely tomentose below, apex acute to mucronate, base tapering, the margins entire, occasionally revolute. Inflorescences subumbellate to corymbose, with clusters of 5 to 10 heads; heads (7- to) 10- to 14-flowered, the peduncles 1–3 mm. long, gray- to brown-pubescent; involucres campanulate, 5.5–7.5 mm. high, 4–7.5 mm. wide, the phyllaries variously pubescent, tomentose on edges, frequently resinous, firmly appressed, gold to brown, frequently with purple tips and more rarely entirely purple, the inner phyllaries narrowly ovate to angular ovate, (4.1–) 4.5–5.1 mm. long, 0.8–1.6 mm. wide, tips acute to blunt, the outer phyllaries ovate to orbicular, 0.6–1.2 mm. long, 0.6–1.2 mm. wide; pappus yellow to purple, inner bristles 5–6 mm. long, outer bristles 0.5–1 mm. long; corollas 6–8 mm. long, white or purple, glabrous, sweet scented; anthers ca. 3 mm. long. Achenes 3–3.5 mm. long, weakly ribbed, glandular. Chromosome number $n = 17$. Flowering and fruiting throughout the year.

DISTRIBUTION. Throughout the higher mountains of Hispaniola, on steep, rocky hillsides and banks, sterile pinelands, and openings in forests, from 600 to 1200 meters (MAP 6).

REPRESENTATIVE SPECIMENS. **Dominican Republic.** AZUA PROV.: Sierra de Ocoa, S.J. de Oca, Los Coroza, *Ekman 11732* (F, TEX, US). BAHORUCO PROV.: El Cercado, S. of town, *Keeley & Keeley 1437–1460* (GA). LA VEGA PROV.: Cordillera Central Constanza, near El Chorro, *Ekman 13966* (F, GH, NY, S, TEX, US). SANTIAGO PROV.: between La Guacara and La Guacarita rivers, La Guacara Arriba, tributary of Boa River, *Liogier 13434* (NY).

Vernonia tuerckheimii was first described by Urban in 1912, on the basis of a specimen collected by Tuerckheim near Constanza in the Dominican Republic. This specimen had distinctly purple-tipped phyllaries and reddish purple pappus bristles. Ekman knew of this species and concurred with Urban on its delimitation. In 1929 Ekman collected several sheets of similar-appearing plants; these, however, had neither the purple-tipped phyllaries nor the reddish pappus of the typical form. From notes attached to these sheets (e.g., *Ekman 11732* S), it appears that he at first felt this was a new species and noted another name (*V. ocana*) on the label; this name was never published. Sometime later when he returned

to Stockholm, Ekman must have discussed these specimens with Urban, as the specimens have annotations by both men, and the name *V. ocana* was replaced by *V. tuerckheimii*. Ekman made notes about this species on the back of several collection labels; for example, on the back of his number *11732*, he says "P.S. *V. tuerckheimii* does not always have purple pappus and is moreover as variable as all Vernonias." From this information it seems fairly clear that *Vernonia tuerckheimii* is the same as, and takes precedence over, the more recently published name for the non-purple plant, *Vernonia microphylla* Alain, which is in every other respect identical to it.

Subsection III. Polyanthes

29. **Vernonia havanensis** de Candolle, Prodr. **5**: 37. 1836. Type: Cuba. Juxta Havanam, *Sagra s.n.* (holotype, G-DC (IDC B–800–2. 769: III. 8!)).

Vernonia cubensis Grisebach, Cat. Pl. Cubens. 144. 1866. Type: Cuba occ. [Cuba], 1863, *Wright 2791* (holotype, GOET!).

Vernonia hieracioides β cubensis (Grisebach) Maza, Anal. Soc. Esp. Hist. Nat. **19**: 268. 1890.

Vernonia stictophylla Wright, Sauv. Anal. Cien. Havana **6**: 176. 1894. Type: Cuba, *Wright 3596* (holotype, GOET!; isotypes, GH!, NY!, US!).

Vernonia cubensis var. *cajalbanensis* Ekman ex Urban, Repert. Sp. Nov. **26**: 101. 1929. Type: Cuba. Pinar del Río Prov., Pinar del Cajalbana, on the very top of the mountain, 28 Aug. 1923, *Ekman 17344* (holotype, S!; isotype, NY!).

Cacalia havanensis (de Candolle) Kuntze, Rev. Gen. Pl. **2**: 970. 1899.

Shrub, 1–2 meters high; stems ribbed, villous to sparsely pubescent, becoming glabrate with age. Leaves crowded along main stems; petioles 1–8 mm. long, pubescent as stems; blades 5–13 cm. long, 1–5.6 cm. wide, length/width ratio ca. 3, widest at or just above the middle, ovate to lanceolate, rarely obovate, shiny, with many glands and short pilose-hispid pubescence, scabrous above, gland dotted and with scattered white hairs below, the apex acute to acuminate, occasionally obtuse, the base rounded to cuneate, the margins entire to denticulate. Inflorescences highly branched cymes, often divaricate with few condensed heads; heads 11- to 24-flowered, the peduncles to 2 cm. long, pubescent; involucres campanulate, 4–7 mm. high, 5–8 mm. wide, the phyllaries resinous, occasionally with scattered hairs on the edges, loosely appressed, in 5 or 6 series, golden to brown, typically with purple tips; the inner phyllaries linear to linear-lanceolate, rarely oblanceolate, 3–5 mm. long, 0.8–1.1(–1.4) mm. wide, tips acute to acuminate with strong central nerve extending into them, the outer phyllaries lanceolate to ovate, 0.8–1.3 mm. long, 1.4–1.8 mm. wide; pappus white to dirty white, inner bristles 4–6 mm. long, outer bristles 0.5–1.2 mm. long; corollas 6–8(–9) mm. long, purple to lavender, resin dotted along the tube; anthers 2.2–3 mm. long. Achenes ca. 2.5 mm. long,

ribbed, resin dotted, with short hairs prominent between the ribs. Flowering and fruiting throughout the year.

DISTRIBUTION. Serpentine ridges, ravines, fields, and open places near rivers and in pine woods, from 300 to 800 meters, in various provinces of Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** MANTANAZAS PROV.: thickets, Cumbre, *Leon, Victorin, & Alain 19726* (NY). ORIENTE PROV.: Baracoa region, Altas de Farola, 35 km. (airline) S. of Baracoa, *Webster 4023* (GH). PINAR DEL RÍO PROV.: Bahía Honda in "cuabales" S. of town, *Ekman 10419* (F, MO, NY, US). SANTA CLARA PROV.: dry field, vicinity of Sopapo, Buenos Aires, Trinidad Mts., *L. B. Smith, Hodgdon, & Gonzales 3357* (GH, US). ISLA DE PINOS: vicinity of San Pedro, *Britton, Wilson, & Selby 14467* (NY, US).

There has been much confusion surrounding this species in the past. Ekman (1914) described *Vernonia cubensis* and *V. havanensis*, here synonymized, but apparently doubted this distinction, saying that "the three species of *V. havanensis* are by no means very good ones. *V. cubensis* Griseb. in many respects is intermediate between *V. havanensis* DC. and *V. hieracioides* Griseb." After examining the available material, I cannot find any consistent differences between the first two species, but I have maintained *Vernonia hieracioides* on the basis of flower number.

30. **Vernonia hieracioides** Grisebach, Mem. Am. Acad. **8**: 511. 1861. TYPE: Cuba. Prope villam Monte Verde, dictam Cuba Orientali, Jan.–July 1859, *Wright 1306* (holotype, K!; isotypes, F!, GH!, MO!, S!, TEX!).

Cacalia hieracioides (Grisebach) Kuntze, Rev. Gen. Pl. **2**: 970. 1891.

Vernonia orientis Gleason, Bull. Torrey Bot. Club **40**: 330. 1913. TYPE: Cuba. Oriente Prov., Sierra de Nipe, near Woodfred, 10 Jan. 1910, *Shafer 3509* (holotype, NY!; isotype, US!).

Shrub, 1–3 meters high; stems ribbed, lanate to pilose-hispid, usually brown. Leaves clustered along stems, especially so below inflorescences; petioles 3–6 mm. long, cinereous-pubescent; blades 3–8.2 cm. long, 0.8–3 cm. wide, length/width ratio ca. 2, widest above the middle, obovate to elliptic-obovate, shiny, gland dotted, variably rugose and sometimes sparingly pilose-hispid above, sparsely pilose-hispid and glandular, with prominent veins below, apex acuminate to occasionally acute or obtuse, base rounded to cuneate, the margins denticulate, with teeth remote. Inflorescences branched, compressed, corymbose, usually with elongate pedicels; heads 5- to 8-flowered, the peduncles 1–10 mm. long, cinereous; involucres campanulate, 4–6 mm. high, 3–6 mm. wide, the phyllaries sparsely strigose to glabrous, conspicuously resin dotted, loosely appressed in 4 to 5 series, gold to brown, often with dark tips, the inner phyllaries oval to oblong-ovate, 2.9–4.2 mm. long, 0.6–1.8 mm. wide, with tips acute to acuminate, ca. 1 mm. long, the outer phyllaries lanceolate to ovate, 0.9–1.8 mm. long, 0.3–1 mm. wide; pappus yellow to brown, inner bristles

(3.5–)4–5 mm. long, outer bristles 0.3–0.5 mm. long; corollas (4.8–) 5–6 mm. long, purple to lavender, glabrous; anthers 2.2–2.8 mm. long. Achenes ca. 2 mm. long, ribbed, with short hairs between ribs, occasionally resin dotted. Flowering and fruiting throughout the year.

DISTRIBUTION. Pine barrens, on serpentine soils, in wet woods, from 400 to 800 meters, in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV.: 5 km. S. of Woodfred, Sierra de Nipe, *Howard 6189* (GH, MO, NY, US); Sierra de Nipe, wet places along Río Piedra in the pinelands, *Ekman 1764* (F, S).

This species superficially resembles *Vernonia havanensis* Grisebach, from which it can be distinguished by its many fewer flowers per head (ca. 6 vs. 12 to 29 in *V. havanensis*) and by its fewer resinous dots on the achenes.

In processing, the collections of *Vernonia hieracioides* and *V. havanensis* were apparently mixed. *Wright 1306* (F, GH, K, MO, S, TEX) are *V. hieracioides*, while those at S, US, and NY are *V. havanensis*.

31. **Vernonia menthaefolia** (Poeppig) Lessing, Linnaea **4**: 268. 1829.

Eupatorium menthaefolium Poeppig ex Sprengel, Syst. Veg. ed. 16. 3: 412. 1826. TYPE: Cuba, 1823, *Poeppig s.n.* (holotype, W, as photo in GH!; isotype, BM!).

Eupatorium perrinianum Sprengel, *ibid.* TYPE: West Indies, *Perrin s.n.* (isotypes, GH!, NY!).

Vernonia ottonis Schultz-Bipontinus, Linnaea **20**: 508. 1847. TYPE: Cuba. Cafetal Fundador, 1839, *Otto 35* (holotype, P!; isotype, GH!).

Vernonia grisebachii Schultz-Bipontinus, Jour. Bot. **1**: 231, 232. 1863. TYPE: Cuba. Fruticose, ascending, fl. white, prope villam Monte Verde dictam, Cuba Orientali, 13 Jan. 1859, *Wright 1305* (holotype, GOET!; isotype, S!).

Vernonia menthifolia var. *grisebachii* (Schultz-Bipontinus) Grisebach, Cat. Pl. Cubens. 144. 1866.

Shrub, 1–2 meters tall; stems ribbed, with minute pubescence. Leaves regularly spaced along main stem, often crowded on lateral branches; petioles 10–15 mm. long, closely pubescent; blades 5–9 cm. long, 1.8–3.5 cm. wide, length/width ratio ca. 3, widest at or slightly below the middle, elliptic to elliptic-ovate, scabrellate, with dense, short hairs on young leaves, their persistent bases on older leaves above, glandular and closely pubescent in younger leaves, sparsely so with age below, apex acute to occasionally acuminate, base rounded, the margins entire to revolute, occasionally denticulate. Inflorescences corymbose, often dense; heads 12- to 20-flowered, the peduncles 3–5 mm. long, closely pubescent; involucres campanulate, 4–6 mm. high, 4–8 mm. wide, the phyllaries resinous, with long, floccose hairs along margins, closely appressed, gold to brown, occasionally with dark tips, the inner phyllaries oblong-lanceolate to oblanceolate, 3.4–4.6 mm. long, 0.6–1.1 mm. wide, with tips acute to acuminate, rarely obtuse, the outer phyllaries ovate, 0.8–1.1 mm. long, 0.4–0.8 mm. wide; pappus tawny with a yellow cast, inner bristles 4.4–5.5 mm. long,

outer bristles 0.5–0.6 mm. long; corollas 6.5–8.5 mm. long, purple to white, resinous, especially at tips of petals, fragrant; anthers ca. 2.5 mm. long. Achenes 2–3 mm. long, ribbed, with numerous short hairs between ribs. Flowering and fruiting throughout the year.

DISTRIBUTION. In thickets, on the edges of savannas near the sea, in woods, between 150 and 1500 meters, La Habana, Santa Clara, Pinar del Río, and Oriente provinces, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** LA HABANA PROV.: Playa de Marianao, *Britton & Wilson 4526* (NY). ORIENTE PROV.: Bayate, Sabana Miranda, edge of the savannah, *Ekman 8568* (F, GH, MO, NY, S, US). PINAR DEL RÍO PROV.: serpentine barrens, Cajalbana, La Palma, *Alain 2375* (NY). SANTA CLARA PROV.: Colonia Limones, Ingenio Soledad, near Cienfuegos, *Pringle 92* (F, GH, MO, NY).

This species is similar in overall appearance to *Vernonia havanensis*, but can be distinguished from it by the shape of the inflorescence and the color of the pappus. The leaves are only rarely toothed in *Vernonia menthaefolia*, not typically so as in *V. havanensis*. Hybrids may occur in the field, and therefore local population studies are needed.

Subsection IV. SAGRAEANAE

32. **Vernonia aronifolia** Gleason, Bull. Torrey Bot. Club 40: 323, 324. 1919. TYPE: Cuba. Pinar del Río Prov., limestone hills, vicinity of Sumidero, 2, 4 Aug. 1912, *Shafer 13514* (holotype, NY!; isotypes, F!, GH!, US!).

Shrub, 1–2.5 meters high; stems closely pubescent to woolly on young twigs, ribbed. Leaves abundant along stem, often crowded beneath heads; petioles 2–5 mm. long, glabrous to sparsely pubescent; blades 5.2–7.5 cm. long, 3.1–3.7 cm. wide, length/width ratio ca. 1.7, widest at or just below the middle, elliptic to ovate, glabrous above, lower surface with short, stiff hairs on lamina, veins prominent, tomentose, apex acuminate, base rounded to tapering, margins remotely spinulose-denticulate. Inflorescences of scorpioid cymes, usually branched at least twice; heads 38- to 66-flowered, sessile; involucres campanulate, 8–10 mm. high, 10–12 mm. wide, the phyllaries closely pubescent, tightly appressed, gold to brown, the inner phyllaries subulate to lanceolate, 8–8.8 mm. long, 1.2–1.7 mm. wide, with tips up to 1 mm. long, stiff, recurved, the outer phyllaries awl shaped, 3.5–5 mm. long, 0.4–1.1 mm. wide; pappus white to dirty white, the inner bristles 7–8 mm. long, the outer pappus of fimbriate scales, 1.5–2 mm. long; corollas 12 mm. long, white, glabrous; anthers 3.5 mm. long. Achenes 3–4 mm. long, resinous, angled but not ribbed. Flowering and fruiting from March to December.

DISTRIBUTION. Limestone hills and steep hillsides, Pinar del Río Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMEN. **Cuba.** PINAR DEL RÍO PROV.: Viñales, among shrubs in Sierra de Viñales, *Ekman 18030* (GH, NY).

The large number of flowers per head, giving the heads the appearance of bursting, is distinctive in this species. It is apparently rare, being confined to rocky limestone areas.

33. Vernonia purpurata Gleason, Bull. Torrey Bot. Club **40**: 322, 323. 1913. TYPE: Cuba. Oriente Prov., Sevilla Estate, near Santiago, Jiquarito Mts., Sierra Maestra, 18 Sept. 1906, *Taylor 544* (holotype, NY!).

Vernonia praestans Ekman & Urban, Repert. Sp. Nov. **26**: 101. 1921. TYPE: Cuba. Oriente Prov., Sierra Maestra, Pico Turquino, 18 April 1915, *Ekman 5508* (holotype, S!; isotypes, GH!, NY!, US!).

Vernonia praestans var. *cacuminis* Borhidi et Muniz, Acta Bot. Acad. Sci. Hungar. **18**: 48. 1973. TYPE: Cuba. Oriente Prov., Sierra Maestra, in pluvi silvis nebulosis muscosis montis Pico Real, cacumen Mt. Pico Turquino, *supra pag.*, 7 Dec. 1969, *Borhidi, Ocujal Muniz, & Vasquez s.n.* (holotype, SV; isotype, BP!).

Shrub, 2–2.5 meters tall; stems striate, thinly tomentose. Leaves often crowded; petioles 2–5 mm. long, closely tomentose; blades 3–6.5 cm. long, 1–3 cm. wide, length/width ratio ca. 3, widest at or slightly above the middle, elliptic to ovate or oblong, shiny, with rigid hairs along main veins and more rarely on blade above, the veins raised, pubescent primarily along those below, the apex obtuse to acuminate, the base rounded, the margins entire, repand, occasionally revolute and with spinulose teeth. Inflorescences corymbose to cymose, usually much condensed; heads 4- to 8-flowered, the peduncles up to 3 mm. long, closely and densely pubescent; involucres narrowly campanulate, (3.5–)4–7 mm. high, 2.5–5 mm. wide, the phyllaries villous, firmly appressed, gold to brown, the inner phyllaries linear-lanceolate, 6.4–6.5 mm. long, ca. 1.5 mm. wide, with tips acute to acuminate, pubescent, the outer phyllaries ovate, 0.5–1.8 mm. long, 0.6–0.8 mm. wide; pappus yellow-brown, inner bristles 6–7.5 mm. long, outer bristles ca. 1.2 mm. long. Achenes angled, glabrous. Flowering and fruiting from April to August.

DISTRIBUTION. Rocky ridges, from 1200 to 2000 meters, Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV. Sierra Maestra: on top of Punta de Palmanoche, S. of Yara, *Ekman 14304* (GH, MO, S); Pico Turquino, *Ekman 5508* (F); Pico Turquino, S. slopes, *Seifriz 1069* (NY).

All specimens of this species, including the type, have very poorly developed heads, none with flowers. The plants appear to resemble *Vernonia pluvialis* of Jamaica and apparently share a similar habitat; *Vernonia pluvialis*, however, has sericeous achenes.

34. Vernonia ekmanii Urban, Ark. Bot. **17**: 62, 63. 1921. TYPE: Haiti. Départ du Sud, prope Civette in collibus siccis, 11 June 1917, *Ekman 223* (holotype, S!; isotypes, F!, NY!, US!).

Shrub, 1–2 meters tall; stems ribbed, covered with dense, white, villous pubescence. Leaves evenly spaced along main stems, not scarce, usually sessile, occasionally with tomentose petioles to 7 mm. long; blades 6.5–10.2 cm. long, 1.8–4.4 cm. wide, length/width ratio ca. 3, widest at the middle, elliptic to linear-lanceolate, rugose, glandular and shiny above, dotted with short, stiff hairs and glands on lamina below, veins on lower surface prominent and villous, the apex acute to mucronate or cuspidate, with tip up to 1 mm. long, the base truncate to oblique, the margins spinulose-denticulate and crenate. Inflorescences of numerous scorpioid cymes, some appearing corymbose; heads 9- to 11-flowered, the peduncles up to 4 mm. long, densely villous; involucres campanulate, 8.5–10 mm. high, 5–7 mm. wide, the phyllaries densely tomentose especially on tips, loosely appressed, gold to brown, the inner phyllaries subulate to linear or linear-oblong; 8–9 mm. long, 1–1.8 mm. wide, sometimes pubescent on inner surface, with tips aristate, up to 1.5 mm. long, usually villous, recurved, the outer phyllaries narrowly deltoid to lanceolate, 1.5–2.3 mm. long, 0.4–1 mm. wide; pappus white, often appearing dirty, inner bristles 6–7.5 mm. long, outer bristles 1.5–2 mm. long; corollas 9–11 mm. long, purple, glabrous; anthers 3.5 mm. long. Achenes 3–4 mm. long, glabrous, with ca. 9 ribs. Flowering and fruiting from December to July.

DISTRIBUTION. In deep ravines, 700 to 1400 meters, Massif de la Hotte, Haiti (MAP 6).

REPRESENTATIVE SPECIMENS. **Haiti.** DÉPART DU SUD: Massif de la Hotte, western group, Torbec, between La Mare Proux and Laurent, *Ekman 5351* (GH, S); in decliv. occidental, mont Ma Blanche, *Ekman 493* (S).

This species appears to be similar to *Vernonia sprengeliana*, which it greatly resembles in overall aspect. The pappus color is highly variable in *V. ekmanii*, a rarer species.

35. **Vernonia sprengeliana** Schultz-Bipontinus, Jour. Bot. London 1: 232, 233. 1863. TYPE: Dominican Republic. Sto. Domingo, 1866, *Bertero 507* (holotype, P!).

Shrub, 1.5–3 meters tall; stems ribbed, covered with a dense, grayish tomentum. Leaves crowded on terminal branches; petioles 1–2 cm. long, densely pubescent; blades 4–10.5 cm. long, 0.6–2.2 cm. wide, length/width ratio ca. 5, widest at or slightly above the middle, lanceolate to linear-lanceolate, rugose to bullate, shiny above, densely tomentose below, apex acuminate to acute, base tapering to subcordate, the margins revolute, repand. Inflorescences of scorpioid cymes, sometimes appearing corymbose, often crowded on terminal branches; heads 9- to 16-flowered, the peduncles 1–5 mm. long, densely pubescent; involucres campanulate, 7–11 mm. high, 5–9 mm. wide, the phyllaries thinly strigose, firmly appressed, gold to brown, often with purple tips, linear to oblong, 6.5–10 mm. long, 0.9–1.5 mm. wide, with tips rounded to mucronate, 1–3 mm. long, the outer phyllaries deltoid, 1–1.5 mm. long, 0.3–0.7 mm. wide; pappus

white or rarely purple tinged, the inner bristles 5–9 mm. long, the outer pappus of fimbriate scales, 0.5–1(–1.5) mm. long; corollas 8–12 mm. long, purple, glabrous; anthers 3.8–4 mm. long. Achenes ca. 4 mm. long, glabrous, angled or faintly ribbed. Chromosome number $n = 17$. Flowering and fruiting throughout the year.

DISTRIBUTION. Rocky hillsides, near towns and disturbed sites, often near water, between 250 and 1250 meters, throughout Hispaniola (MAP 6).

REPRESENTATIVE SPECIMENS. **Dominican Republic.** BARAHONA PROV.: Las Salinas a Los Churos, *Fuertes 1388* (F, GH, NY, US). LA VEGA PROV.: vicinity of Piedra Blanca, along Duarte Hwy. near dam, *Allard 14753* (MO, US). **Haiti.** DÉPART DE L'ARTIBONITE: Ennery, *Ekman 2460* (NY, S, TEX). DÉPART DU NORD: vicinity of St. Michel de l'Atalaye, *Leonard 7601* (MO, US).

Vernonia sprengeliana is among the most easily recognized species in the West Indies. From a distance it can be identified by the bright flower clusters in a subcorymbose arrangement. This species is closely allied to *V. ekmanii*.

36. **Vernonia viminalis** Gleason, Bull. N. Y. Bot. Gard. **4**: 184. 1906.
TYPE: Cuba, *Wright 285* (holotype, NY!; isotype, GH!).

Shrub, ca. 1 meter high; stems with dense gray-white tomentum. Leaves evenly spaced along main stems; petioles up to 4 mm. long, densely villous; blades 8–14 cm. long, 1–3 cm. wide, length/width ratio ca. 4, widest at or slightly below the middle, elliptic to narrowly oblong, shiny, with sparse pubescence of long, white hairs above, softly white-pilose beneath, with densest tomentum on veins of lower surface, apex acuminate to acute, base rounded to nearly cordate, margins minutely denticulate. Inflorescences of extended scorpioid cymes, subbracteal leaves well developed; heads 23- to 30-flowered, sessile; involucres campanulate, 10 mm. high, 10 mm. wide, the phyllaries densely villous, firmly appressed, gold to brown, the inner phyllaries oblong to linear-lanceolate, 8.5–9.5 mm. long, 0.9–1.2 mm. wide, with tips cuspidate, often recurved, the outer phyllaries deltoid to subulate, 1.8–2 mm. long, 0.4–0.5 mm. wide; pappus white, inner bristles 6.5–7.5 mm. long, outer bristles 0.8–1 mm. long; corollas 10 mm. long, purple, glabrous; anthers 3–3.5 mm. long. Achenes 3–4.5 mm. long, glabrous, angled. Flowering and fruiting dates not recorded on collections.

DISTRIBUTION. Limestone areas, Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMEN. Only the type specimen was available for measurement and scoring.

Wright's collection number *285* was apparently mixed up in processing and actually contains two species, *Vernonia viminalis* and *V. sagraeana*. The same numbers are, therefore, listed under both species; *Wright 285* in

NY and GH is *V. viminalis*, while this number in GOET, F, MO, TEX, and S represents *V. sagraeana*. *Vernonia viminalis* has conspicuous long, white hairs on the leaves, while *V. sagraeana* is glabrous. It is possible that *V. viminalis* is a hybrid or simply an unusual variant of a more common species; more collections are needed.

37. **Vernonia wrightii** Schultz-Bipontinus, Jour. Bot. London 1: 234. 1863. TYPE: Cuba. In prope Villam Monte Verde, dictam, Cuba Orientali, Jan.–July 1859, *Wright 284* (holotype, P; isotypes, GH!, K!).

Vernonia leptoclada sensu Gleason, Bull. N. Y. Bot. Gard. 4: 183. 1906, non *V. leptoclada* Schultz-Bipontinus, 1863.

Shrub, 1–4 meters tall; stems densely tomentose. Leaves often crowded on main stems; petioles to 5 mm. long, densely pubescent; blades (2.1–)4–8.4 cm. long, 0.7–3.6 cm. wide, length/width ratio ca. 3, widest at or below the middle, elliptic to linear-lanceolate, firm, shining and glabrous above, finely pubescent and resinous below, hairs prominent on veins of lower surface, apex obtuse to acute or acuminate, base rounded to subcordate, the margins entire, repand, occasionally spinulose-denticulate. Inflorescences of scorpioid cymes; heads (15- to) 17- to 26- (to 29-) flowered, sessile; involucres campanulate, 7.5–10 mm. high, 8–12 mm. wide, the phyllaries pubescent, becoming glabrate with age, firmly appressed, gold to brown, the inner phyllaries linear to subulate, (6–)7–8.5 mm. long, 0.9–1.6 mm. wide, with tips reflexed, subulate, to 5 mm. long, the outer phyllaries ovate to lanceolate, 1–3 mm. long, 0.4–1.1 mm. wide; pappus tawny brown, often with a pinkish cast, inner bristles 5–6(–7.5) mm. long, outer bristles ca. 1 mm. long; corollas 8–9 mm. long, purple to white, glabrous; anthers 2.5–3.5 mm. long. Achenes ca. 3 mm. long, remotely angled, with a few ribs, rarely with a few short hairs. Flowering and fruiting throughout the year.

DISTRIBUTION. Savannahs, pinelands, and mountainsides, between 300 and 900 meters, in Oriente Province, Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE PROV. Baracoa: pineland hill N. of El Yunque, *Ekman 3541* (F, GH, NY, S); in carrascales on the path to Florida, *Ekman 3500* (F, GH, MO, US).

The true identity of *Vernonia wrightii* has had a long and rather confused history due to the interchange of labels on Wright's specimens numbered *284* and *1309* (see Ekman, 1914, pp. 16, 17, 73, for a full discussion). Wright's collections numbered *284* that are dated 1859 are *V. Wrightii*; those dated 1856–57 are *V. sagraeana*.

38. **Vernonia sagraeana** de Candolle, Prodr. 5: 55. 1836. TYPE: Cuba. Circa Havanam, *Sagra 663* (holotype, G-DC (IDC B–800–2. 775: I. 2!)).

Vernonia valenzuelana Richard in Sagra, Hist. Fis. Pol. Cuba (Paris) **11:** 33, 34. 1850. TYPE: Cuba. Crescit in Vuelta de Abajo, *Valenzuela s.n.* (holotype, P!; isotype, S!).

Vernonia rubricaulis sensu Grisebach, Mem. Am. Acad. **8:** 511. 1861, non *V. rubricaulis* Humboldt & Bonpland, 1810.

Vernonia inaequiserrata Schultz-Bipontinus, Jour. Bot. London **1:** 232. 1863. TYPE: Cuba, 1860, *Wright 285* (holotype, P; isotypes, F!, GOET!, MO!, NY!, TEX!).

Vernonia rigida Swartz var. *sagraeana* (de Candolle) Grisebach, Cat. Pl. Cubens. 144. 1866.

Vernonia rigida Swartz var. *valenzuelana* (Richard) Grisebach, *ibid.*

Vernonia inaequiserrata Schultz-Bipontinus var. *obtusifolium* Grisebach, *ibid.* TYPE: Cuba. In Cuba Orientali, 1861, *Wright 285*, pro parte (holotype, GOET!).

Vernonia inaequiserrata var. *angustifolia* Grisebach, *ibid.* TYPE: Cuba. In Cuba Orientali, 1861, *Wright 2784* (holotype, GOET!; isotypes, GH!, MO!, NY!, TEX!).

Vernonia fallax Gleason, Bull. Torrey Bot. Club **40:** 324, 325. 1913. TYPE: Cuba. Santa Clara Prov., Trinidad Mts., Arroyo Grande to Trinidad, 12 March 1910, *Britton & Wilson 5478* (holotype, NY!).

Vernonia aceratoides Gleason, *ibid.* TYPE: Cuba. In Cuba Orientali, 1861, *Wright 2784* (holotype, MO!; isotypes, GH!, NY!, TEX!).

Vernonia angusticeps Ekman, Ark. Bot. **13:** 14, 15. 1914. TYPE: Cuba, 1856–57, *Wright 284* (holotype, G!; isotypes, F!, GH!, MO!).

Vernonia linguaefolia Ekman, *ibid.* 19, 20, p.p. TYPE: Cuba. In Cuba Orientali, 1860–64, *Wright 285* (holotype, S!; isotype, S!).

Vernonia sagraeana de Candolle var. *angusticeps* (Ekman) Gleason, Bull. Torrey Bot. Club **46:** 240. 1919.

Vernonia reedii Ekman & Urban, Repert. Sp. Nov. **26:** 97. 1929. TYPE: Cuba. Santa Clara Prov., Lomas del Banao, El Purial on Río Banao, in rocky places on top of "El Purial," 27 Jan. 1923, *Ekman 16227* (holotype, S!; isotypes, F!, GH!, NY!).

Vernonia potrerillona Ekman & Urban, *ibid.* 98. TYPE: Cuba. Santa Clara Prov., in montibus Liguanea Trinidad in cacumine Pico Potrerillo, Mart. fruct., *Ekman 18956* (holotype, S!; isotype, NY!).

Shrub, 1–2 meters high; stems ribbed, closely and densely pubescent. Leaves evenly spaced along main stem, more crowded under inflorescences, sessile or with pubescent petioles to 3 mm. long; blades 5–10.5 cm. long, 0.7–3.4 cm. wide, length/width ratio ca. 3, but variable, widest at the middle, elliptic, shiny, pubescent to glabrate above, closely tomentose and resinous below, pubescence decreasing with age on lower surface of blade but persistent on veins, apex obtuse to acute or acuminate, base rounded to cuneate, the margins entire to remotely denticulate, revolute to repand. Inflorescences of scorpioid cymes, often extended; heads (8- to) 11- to 25-flowered, sessile or rarely with densely pubescent peduncles to 2 mm. long; involucres campanulate, 6–10 mm. high, 5–11 mm. wide, the phyllaries villous, most pubescence near tips, loosely appressed, gold to brown, the inner phyllaries lanceolate to linear, 5.3–7.9 mm. long, 0.9–1.3 mm. wide, with tips acuminate, rarely recurved, the outer phyllaries del-

toid, 1–2 mm. long, 0.4–1 mm. wide; pappus white, the inner bristles 5.5–7 mm. long, the outer pappus of fimbriate scales, 1–1.5 mm. long; corollas (8–)9–9.5 mm. long, purple or white, glabrous; anthers 3–3.5 mm. long. Achenes 3–4 mm. long, glabrous, angled when mature. Flowering and fruiting throughout the year.

DISTRIBUTION. Hillsides and disturbed areas, 500 to 1200 meters, in much of Cuba (MAP 4).

REPRESENTATIVE SPECIMENS. **Cuba.** LA HABANA PROV.: Camp Florida, in "Cuabales" at Río Quezada, *Ekman 13576* (GH, NY, S). ORIENTE PROV.: Sierra Maestra, above Daiquiri, *Ekman 8052* (F, GH, S). PINAR DEL RÍO PROV.: Pinar de Cajalbana on E. slope of mt., *Ekman 17361* (M, S, US). SANTA CLARA PROV.: Lomas del Banao, Loma del Obispo, *Ekman 16280* (F, S).

Vernonia sagraeana is a highly variable species that has been separated into entities many times on the questionable basis of leaf shape, but rarely on the more reliable basis of flower number. Leaf size and shape are highly variable in all vernonias, and are not generally good key characters at the species level.

Subsection V. PALLESCENTES

39. **Vernonia pallescens** Gleason, Bull. N. Y. Bot. Gard. 4: 192, 193. 1906. TYPE: St. Vincent. Mountains at 2000 ft. and above; nowhere common, *Smith & Smith 992* (holotype, NY!; isotype, K!).

Shrub, 1–2 meters tall; stems ribbed, with inconspicuous, finely hispid pubescence. Leaves large, well spaced, appearing to be almost basal; petioles 5–10 mm. long, minutely pubescent to glabrate; blades 7.8–23.5 cm. long, 2.7–6 cm. wide, length/width ratio ca. 3, widest at the middle, elliptic, minutely puberulent and resin dotted above, shiny and often sparsely pubescent and resinous below, expanded and membranous, apex long-acuminate, base cuneate, the margins serrate, particularly on upper half of leaf. Inflorescences of extended scorpioid cymes, subbracteal leaves not present; heads (9- to) 10- to 13-flowered, sessile; involucres campanulate, (4.5–)5–6 mm. high, 4–6 mm. wide, the phyllaries minutely strigose, loosely appressed, gold to brown, frequently with dark tips, the inner phyllaries ovate to oblong, (3.7–)4–5 mm. long, 0.8–1.2 mm. wide, tips acuminate to obtuse, the outer phyllaries lanceolate to ovate, 1–1.9 mm. long, 0.4–0.6 mm. wide; pappus pale brown, inner bristles 4–4.5 mm. long, outer bristles 0.5–1 mm. long; corollas 5–6 mm. long, purple to white, resin dotted; anthers 1.5(–2) mm. long. Achenes ca. 2 mm. long, obscurely ribbed, sericeous. Flowering and fruiting from March to May.

DISTRIBUTION. Mt. Grand Bonhomme and the mountains near the Châteaubelair River, between 400 and 800 meters, St. Vincent (MAP 2).

REPRESENTATIVE SPECIMENS. **St. Vincent.** Valley of S. fork of the Cumberland River, *Morton 5794* (US); mts. above the Châteaubelair River, *Morton 5276* (GH, US); ESE. ridge of Mt. Grand Bonhomme, *Proctor 26060* (TEX).

This species is distinct from all other West Indian vernonias because of its serrate, membranous leaves. It also has a distinctive pollen type, intermediate between the other major pollen types in the West Indies (Keeley & Jones, 1977a).

Subsection VI. Scorpioides

40. **Vernonia scorpioides** (Lamarck) Persoon, Syn. Pl. **2**: 404. 1807.

Conyza scorpioides Lamarck, Encycl. Méthod. **2**: 88. 1786. Type: Brazil, *Commerson s.n.* (holotype, P-JU (IDC B–6206–2. 621: I. 3!)).
Vernonia subrepanda Persoon, *ibid.* Type: Brazil, *Commerson s.n.* (holotype, P-JU (IDC B–6206–2. 621: I. 3!)).
Vernonia tournefortioides HBK. Nov. Gen. Sp. (quarto ed.), 34, 35. 1818. Type: Venezuela. Caracas, *Humboldt s.n.* (holotype, B, as photo B!).
Lepidaploa scorpioides Cassini, Dict. Sci. Nat. **2**: 16. 1823.
Staehelina solidaginoides Willdenow ex Lessing, Linnaea **4**: 281, 282. 1829. Type: Venezuela. Caracas, *Humboldt s.n.* (holotype, B, as photo B!).
Vernonia flavescens Lessing, *ibid.* **6**: 657. 1831. Type: Brazil, *Commerson s.n.* (lectotype (here designated), P-JU (IDC B–6206–2. 621: I. 3!)).
Vernonia scorpioides Persoon α *centriflora* de Candolle, Prodr. **5**: 42. 1836. Type: Brazil. Bahia, April 1831, *M. d'Hostky s.n.* (lectotype (here designated), G-DC (IDC B–800–2. 771: I. 6!)).
Vernonia scorpioides β *subrepanda* (Persoon) de Candolle, *ibid.*
Vernonia scorpioides (Persoon) γ *subtomentosa* de Candolle, *ibid.* Type: Brazil, 1834, *M. Lund 479* (lectotype (here designated), G-DC (IDC B–800–2. 771: II. 8!)).
Vernonia scorpioides (Persoon) δ *longifolia* de Candolle, *ibid.* Type: Brazil. Bahia, 1830, *M. Salzman s.n.* (holotype, G-DC (IDC B–800–2. 771: III. 1!)).
Vernonia scorpioides ε *longeracemosa* de Candolle, *ibid.* Type: Brazil, 1832, *Poeppig 33 (1203)* (lectotype (here designated), G-DC (IDC B–800–2. 771: III. 3!)).
Vernonia longeracemosa Martius ex de Candolle, Prodr. **5**: 42. 1836.
Vernonia lanuginosa Gardner, Jour. Bot. London **5**: 219. 1846. Type: Brazil. Minas Gerais Prov., in fruticetis prope Formigas in Sertão, July 1840, *Gardner 4764* (holotype, BM!; isotype, NY!).
Vernonia saepium Ekman, Ark. Bot. **17**: 63. 1922. Type: Haiti. Départ du Sud, Morne de la Hotte ad Ma Blanche, prope Dayette, 7 Aug. 1917, *Ekman 463* (holotype, S!; isotypes, F!, GH!, NY!, S!, US!).
Cacalia tournefortioides (HBK.) Kuntze, Rev. Gen. Pl. **2**: 971. 1891.
Cacalia scorpioides (Lamarck) Kuntze, *ibid.*

Shrub, upright or sprawling, 1–3 meters high; stems densely pubescent, strigose to villous, ribbed. Leaves numerous, but not crowded along main stems; petioles 4–7(–10) mm. long, densely gold-pubescent; blades (1.8–)3.3–9.5 cm. long, (1.2–)2.2–6 cm. wide, length/width ratio ca. 1.5, widest at or below the middle, ovate to elliptic, some very broad, strigose to pilose-hispid and shiny above, hispid to hirsute below, tomentum densest in young leaves, the apex obtuse to acute or acuminate, the base cuneate, tapering, the margins entire to rarely denticulate. Inflorescences of

scorpioid cymes, heads very close together; heads (14- to) 16- to 22-flowered, sessile or with woolly-pubescent peduncles to 1 mm. long; involucres campanulate, 3.5–4.5(–6) mm. high, 4–7 mm. wide, the phyllaries firmly appressed, with long hairs at margins, gold to green, the inner phyllaries often purple tinged and pubescent, linear-lanceolate with curled tips, 3.8–4.5 mm. long, 0.6–1.2 mm. wide, the curled tips 0.2–0.5 mm. long, the outer phyllaries lanceolate with a much-constricted base, 1–2 mm. long, 0.5–0.8 mm. wide; pappus white, the inner bristles 4.5–6 mm. long, the outer pappus of fimbriate scales, (0.8–)1–1.6 mm. long; corollas 6–7(–8) mm. long, purple to white, outer tips of petals with conspicuous white hairs often projecting into the clefts between the corolla lobes; anthers 1.5–2 mm. long. Achenes 1.5 mm. long, with sparse, stiff hairs between ribs. Flowering and fruiting from March to August.

DISTRIBUTION. Open places, along disturbed roadsides, and near the ocean and towns, in Trinidad and Tobago and Haiti (MAP 5).

REPRESENTATIVE SPECIMENS. **Haiti.** DÉPART DU SUD: Massif de la Hotte, Torbec, Forman, *Ekman 7587a* (F). **Tobago:** near Little Bacolet Bay, *Howard 10459* (GH, NY). **Trinidad:** North Post Rd., *Britton, Hazen, & Mendelson 776* (GH).

This species has a very characteristic aspect both in the field and in the herbarium, with its dense scorpioid cymes and broad leaves that are often folded. The corollas are also conspicuous because they are hairy, a feature unknown in other West Indian vernonias. The range of this species extends throughout much of South America.

Subsection VII. PANICULATAE

41. **Vernonia blodgettii** Small, Flora S.E. U.S. 1160. 1903. Synonymies, typifications, and representative specimens given in Keeley and Jones (1977b).

Herbaceous perennial, 1–1.5 meters high; stems erect, glabrous, often branched at base. Leaves mostly basal, sessile; blades 1.8–6.9 cm. long, 0.1–1 cm. wide, linear or nearly so, glabrous above, lightly gland dotted below, apex obtuse to acute, base attenuate, the margins slightly revolute, entire. Inflorescences loose, irregular, with few heads; heads about 21-flowered; involucres loosely and irregularly imbricated, campanulate, 5–8.5 mm. high, 5.5–10.5 mm. wide, the phyllaries firmly appressed, deltoid to lanceolate, the inner phyllaries 3.9–6.7 mm. long, the outer phyllaries 1.7–3.5 mm. long, purple, glabrous to slightly pubescent, with tips acute to subacute, 0.1–0.5 mm. long; pappus light yellow, the inner bristles 5.5–7.8 mm. long, the outer pappus of fimbriate scales, 0.5–0.8 mm. long. Achenes pubescent, ribbed, 2.3–2.7 mm. long. Chromosome number $n = 17$. Flowering and fruiting from January to July.

DISTRIBUTION. Limestone soils and pinelands, in Florida and the Bahamas.

SECTION TEPHRODES

42. Vernonia cinerea (Linnaeus) Lessing, Linnaea 4: 291. 1829. Synonymies, typifications, and representative specimens given in Keeley and Jones (1977b).

Annual, 3–6 dm. high; stems tomentulose with T-shaped hairs, sometimes becoming glabrate with age. Leaves scattered along stem; petioles margined, ca. 1.5–2.5 cm. long, pubescent; blades 1.5–2.5 cm. wide, 2–5 cm. long, lanceolate, pubescent above, pubescent with T-shaped trichomes and punctate beneath, apex acute, base attenuate, margins remotely toothed. Inflorescences of loose, open, and often spreading cymes; heads 12- to 16-flowered; involucres campanulate, 6–7 mm. high, 5–6 mm. wide, phyllaries loosely and irregularly imbricate, the inner phyllaries linear-oblong, 5–5.5 mm. long, 0.6–0.8 mm. wide, with acuminate to subulate purplish tips, the outer phyllaries 0.5–1 mm. long; pappus white, deciduous, inner bristles ca. 4 mm. long, outer bristles ca. 0.2 mm. long; corollas purplish lavender, 6–7 mm. long. Achenes rounded, nearly ribless, ca. 1.5 mm. long. Flowering and fruiting throughout the year.

DISTRIBUTION. Antigua, Bahama Islands, Cuba, Curaçao, Dominica, Dominican Republic, Grand Cayman, Grenada, Guadeloupe, Haiti, Jamaica, Martinique, Montserrat, Netherlands Antilles, Puerto Rico, St. Lucia, St. Kitts, St. Vincent, Tortola, Trinidad and Tobago, Virgin Islands. This species is extremely weedy and is found in almost all disturbed habitats.

EXCLUDED SPECIES

Vernonia anthelmintica (L.) Willd. Sp. Pl. 3: 1634. 1804. This Old World species is a well-known *Vernonia* that was imported to Jamaica for its medicinal properties. It was collected at Green Harbour at the turn of the century, but has not been re-collected since. For this reason it is not included in this treatment.

Vernonia tetrantha (Urban) Ekman, Ark. Bot. 13: 8, 9. 1914. This taxon was described under *Piptocarpha* and has not been reevaluated since Ekman's study. It may well be a *Vernonia*, but a decision awaits further study because the detailed comparison of genera is beyond the focus of the present study.

Ekmania lepidota (Griseb.) Gleason (Bull. Torrey Bot. Club 46: 250. 1919) was previously treated under *Vernonia*. Gleason noted the unusual ring of fused outer pappus scales in this species and removed it from *Vernonia* to *Ekmania*. It appears to be distinct.

Two species of subsection GRACILES have been reported to occur in the West Indies. These are *Vernonia gracilis* HBK. subsp. *tomentosa* Ekman and *V. tricephala* Gardner. There is only one record of *Vernonia gracilis* subsp. *tomentosa* from Bequia, a small island in the Grenadines, in 1889

(*Dalton & Smith 288*, K). It is possible that this plant was collected there, but it has not been re-collected since. *Vernonia gracilis* subsp. *gracilis* is found in Colombia near the Caribbean, and in Brazil; it may be that the West Indian location was in error or that the plant was adventive on Bequia. *Vernonia tricephala*, likewise, is found principally in South America. It was collected around the turn of the century at Cedros, Trinidad (*Broadway 2174*, G-DC), but has not been reported since.

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Preliminary Announcement

Thirteenth International Botanical Congress

Sydney, Australia. 21-28th August, 1981

The Programme will consist of 12 sections — molecular, metabolic, cellular and structural, developmental, environmental, community, genetic, systematic and evolutionary, fungal, aquatic, historical, and applied botany. There will be plenary sessions, symposia, and sessions for submitted contributions (papers and posters). Chairman of the Programme Committee:—Dr. L. T. Evans.

Field Trips will include visits to arid and semi-arid regions, eucalypt forest, rain forest, heath, coastal vegetation (e.g. Great Barrier Reef, mangroves) etc., and specialist trips. Chairman of the Field Trips Committee:—Prof. L. D. Pryor.

First Circular, containing details, will be mailed in August, 1979. Send your name and full address, preferably on a postcard, to ensure your inclusion on the mailing list.

Enquiries should be sent to the Executive Secretary, Dr. W. J. Cram.

Congress address — 13th I.B.C., University of Sydney, N.S.W. 2006, Australia.

Sponsored by the Australian Academy of Science.

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